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Founded by J. A. Nieuwland, C.S.C.

Arthur L. Schipper, *Editor*

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A Study of the Southern Woodchuck, Marmota monax monax

Roy A. Grizzell, Jr.

Kentucky Woodlands Refuge, Golden Pond, Ky.

The investigations reported here were started in the summer of 1947 and carried through the summer of 1949. Intensive studies were made on specific areas of the Patuxent Research Refuge, Laurel, Maryland. Incidental observations were made on other parts of the Refuge, at several locations in Maryland, and near Ann Arbor, Michigan.

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I am grateful to the Wildlife Management Institute which supported this project through a fellowship, and to the U.S. Fish and Wildlife Service for a Research Collaborator's appointment making available the many facilities of the Patuxent Research Refuge. To the Director of the Refuge, Mr. Arnold L. Nelson, and the entire staff go my thanks for their valuable assistance. Work at the Refuge was a part of the Wildlife on Agricultural Lands Project under the capable leadership of Dr. Durward L. Allen and Mr. Oscar Warbach. Words cannot express the appreciation that I owe them for their interest and guidance. To other members of the Refuge staff: Dr. A. C. Martin, Mr. L. M. Llewellyn, Mr. F.M. Uhler, and Dr. J. P. Linduska I am very grateful. To Dr. Warren W. Chase, the chairman of my graduate committee, I am indebted for help and advice throughout the entire course of the program. Other members of the committee, Dean S. T. Dana, Dr. E. C. O'Roke, Dr. S. A. Graham, and Dr. E. T. Hooper graciously contributed their time and advice.

Naturalists have known of the woodchuck since at least the early 1700's, but except for a few life history notes and accounts of the animal in travel journals very little was written about the animal until 1884 when Merriam published his account of the mammals of the Adirondack region in New York. Seton (1929) and Howell (1915) have furnished information about the groundhog. Hamilton (1934) in his study of the life history of the rufescent woodchuck in New York has made an important contribution to our knowledge of the animal. Other authors, too many to mention here, have added greatly to an understanding of this important animal by reporting their observations of life history, methods of control, and hibernation.

STUDY AREA

The Patuxent Research Refuge of the U.S. Fish and Wildlife Service is located between Laurel and Bowie, Maryland, about 20 miles northeast of Washington, D.C. The Patuxent River flows through the area northwest to southeast and drains the Refuge and surrounding territories. The Agricultural Research Center of the Department of Agriculture is located to the west and Fort George G. Meade adjoins the area along the northeast boundary. Private holdings border the northwestern and eastern boundaries.

Most of the intensive work during the investigation was carried out at two different areas of the Refuge, these having been designated as Conservation Farm A and Check Farm B.

Hotchkiss and Stewart (1947) have described the vegetation of the Refuge. All plant associations on the two farms represent types that have recovered from previous cultivation. After a field has been abandoned, the annual weeds come in followed by perennials. Fallow fields show a preponderance of broomsedge (*Andropogon virginicus*) and scrub pine (*Pinus virginiana*) after two or three years. Pure stands of scrub pine and sweetgum (*Liquidambar styraciflua*) are eventually replaced by southern red oak (*Quercus falcata*) and the pin oak-red maple (*Quercus palustris-Acer rubrum*) types respectively. Black Locust (*Robinia pseudoacacia*) is also an early invader of upland fields, often mixed with scrub pine.

Hedgerows, favorite habitats of the woodchucks and several other species of farm wildlife, contain such typical plants as blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), grape (*Vitus* spp.), sumach (*Rhus* spp.), black cherry (*Prunus serotina*), persimmon (*Diospyros virginiana*), and sassafras (*Sassafras albidum*).

METHODS

Information regarding woodchucks was obtained mainly by live-trapping, supplemented by shooting, den excavation, observation, tracking, and holding animals under simulated natural conditions in pens.

For the best trapping results a live-trap was placed at the entrance to a woodchuck burrow. If placed close to the den the animal inhabiting the burrow was usually caught, but if placed more than 10 yards away the trap was frequently ignored. Sometimes a trap placed next to a burrow would fail to catch the 'chuck, therefore a new technique was developed to catch these few wary animals. A rectangular hole was dug in front of the main burrow entrance so that the trap would fit snugly against the entrance. Other exits were plugged and almost invariably the trap would contain the woodchuck by the next day. The 'chucks showed little inclination to dig out around the traps.

The trap used in the investigation is a modification of the old cat-trap used by the Biological Survey. Ear corn and smoked herring were placed in all traps as bait. The two baits used are easy to handle, will not rot or wilt rapidly, and are inexpensive. One or the other proved acceptable to all farm game and fur animals encountered on the study areas. Traps should be placed in the shade whenever possible during the summer. In hot weather woodchucks, squirrels, weasels, and young rabbits will frequently succumb if temperatures reach 80-85° F without shade.

To handle the animals, several methods were used during the study. A wire cone, a gunny sack and finally a cotton mesh bag were used. The wire cone was found to be practical but soon was chewed by the animals and rendered useless. In spite of the necessity of continual repairs, the wire cone was found to be the most satisfactory for handling raccoons. A gunny sack was the most practical for handling skunks but was rather cumbersome for woodchucks and other farm game. A cotton mesh fish-bag of sturdy knotted twine, one-inch meshes, draw-string top in a 20 x 30 inch size was found to be the most practical. The bag is also by far the best device for handling squirrels and rabbits. The ear can easily be pulled through the mesh for tagging. Sexing, aging, weighing, and examinations can all be facilitated by using the mesh bag. See figs. 1-4 for details on handling the woodchuck.

Fig. 1.—Preparing to transfer woodchuck from trap to handling bag

The animals were marked on both ears by using a style 1005 no. 3 tag marketed by the National Band and Tag Company of Newport, Kentucky. During the two years of the study, only one animal has been known to pull both tags out. It was found best to turn the tag through the ear after application, thereby lessening the chance of infection and facing the tag so that the numbers may be easily read.

The applications of tags through the ear pinna sometimes cause infections, particularly among fossorial animals and in localities where wood ticks are numerous. An experiment testing the effectiveness of an alcohol-sulfanilamide mixture for the prevention of infections was tried. Results indicated that preventive application was not necessary. The solution did prove effective in clearing up infections that had already started.

Two types of holding pens were constructed for use in breeding and hibernating studies. One type resembled that used by Hamilton (1934). A much larger holding pen that could be used for year-round observations and experimental studies was also constructed. Two cages were constructed side by side, the dimensions of each cage being 5′ wide, 20′ long, and 5′ high. The wire extended into the ground and was laid under each cage to prevent the animals from escaping by burrowing through the soil. Each pen was provided with a

Fig. 2.—Animal secured in handling bag

wooden burrow leading into a box lined with dry hay to simulate as near as possible natural conditions. Observations were made on hibernation and breeding.

DESCRIPTION OF THE ANIMAL

The woodchuck belongs to the order Rodentia, family Sciuridae, subfamily Sciurinae, and genus *Marmota*.

Howell (1915) recognized the following subspecies of *Marmota monax: monax* (Linnaeus), *rufescens* Howell, *preblorum* Howell, *ignava* (Bangs), *canadensis* (Erxleben), *petrensis* Howell, and *ochracea* Swarth.

Since Howell's revision two new subspecies have been added. Black (1935) described *M. m. bunkeri* and gave its range as northeastern Kansas and probably extending north into Nebraska and west in Kansas up the rivers for a considerable distance. Anderson (1943) added *M. m. johnsoni*, and gave its range as the Gaspé Peninsula, Quebec, from Percé at sea level up to about 1600 feet near the head of the Grand Cascapedia River.

Howell (1915) in differentiating the southern woodchuck from other subspecies gave the type locality as Maryland and recognized the following characters: "Underparts of mixed colors (grizzled), sides of neck without conspicuous buffy patches, tail brown or black, colors pale (underfur on back light pinkish cinnamon to light gray at tips; belly not deep red), skull large; condylo-basal length more than 90 mm."

According to a newspaper clipping, on file at the U.S. National Museum, *woodchuck* as applied to the groundhog, is not a compound of *wood* and *chuck* as commonly supposed. It is a corruption of the Indian word *wejack*, *woodshaw*, or *woodchoock*, a name applied to this animal by hunters, trappers, and traders in the Hudson Bay region. Supposedly the word is derived from the Cree *otcheck* or the Chippewa *otchig*, which was applied to the fisher by the Indians, but which was transferred to the groundhog by the whites. The Bureau of American Ethnology notes that in the fur nomenclature of the Hudson's Bay Company, the skins of groundhogs have long been known as *woodchucks*.

Various color phases have been described by Cahalane (1947) and Hamilton (1934).

Fig. 3.—Ear tag being inserted

No albinos or true melanistic phases have been observed during the present study. One old male was often trapped that had a decided grizzled appearance.

Some pelage differences were noted among animals living in different habitats. Several animals trapped on a wooded hammock or a flood plain swamp near the Patuxent River indicated pelage differences from the animals handled on the farm areas about a mile away. The soil on the hammock was an orange-yellow clay loam and the underfur of the woodchucks inhabiting the areas closely resembled the color of the soil, the underfur being brighter than that of the farm animals. The color was not due to the actual presence of soil attached to the fur.

Malocclusions are occasionally found among woodchucks but none was observed during the present investigation.

DISTRIBUTION

According to Howell (1915) the southern woodchuck is distributed through the "middle eastern United States from Pennsylvania, New Jersey (?), Ohio, Indiana, and Iowa, south to the northern parts of South Carolina, Georgia, Alabama, and Arkansas; west to Eastern Kansas."

Burt (1943) reviewed materials in the collections of the University of Michigan Museum of Zoology and concluded that the specimens from the Lower Peninsula of Michigan were intergrades between *monax* and *rufescens* but more closely resembled *monax*. He saw no valid reason for recognizing two races in lower Michigan. Burt's work has pointed up the pressing need for a complete revision of the woodchucks.

The largest populations at the present time seem to be in the Middle Atlan-

Fig. 4.—Obtaining the weight of a woodchuck

tic States of Maryland and Pennsylvania. An interesting extension of range has occurred on the Eastern Shore of Maryland within the present century. Mr. Ray Prettyman has kept records which show that the woodchuck first appeared there shortly after the turn of the century, spreading down from Pennsylvania. Recently populations have increased in the vicinity to the extent that they constitute a problem in some areas. The range extension has progressed to the flat coastal plain.

Scott (1937) reports a northward extension of the southern woodchuck into Iowa along wooded streams.

Figure 5 shows three white, nipple-like organs, which are located just inside the anus. When the animal is excited the glands are everted and a musky

Fig. 5.—Ventral view of woodchuck showing anal glands

SCENT GLANDS

odor is disseminated. The gland secretion is not sprayed in small droplets as in the skunk. No visible liquid is secreted but the odor can easily be detected. It is doubtful that the odor has any actual repelling qualities towards other animals. As far as is known, the only value of the scent glands to woodchucks is for purposes of communication. I have many times identified the occupant of a den as a woodchuck by the characteristic odor. During the breeding season the odor is probably a definite factor in enabling males to locate the females. Hamilton (1934) gives an interesting account of scent glands being used for communication. While waiting for some woodchucks to put in their appearance, he noticed the peculiar odor always associated with the animals. Immediately after the smell was noticed several animals put in their appearance. A little later more 'chucks came out, again preceded by the characteristic odor.

VOICE

The woodchuck is often referred to as a *whistle pig*. The name may be somewhat misleading, for the woodchuck's whistle is not often heard by the casual observer. The hoary marmots of the Rocky Mountains are much more vocal than the southern woodchucks. The whistle is given either to warn other animals of danger or when the 'chuck is excited. The whistle itself is a short, sharp, piercing note followed by a series of hiss-like noises that are emitted while the animal trembles all over. The performance is preceded by a quick movement of the head. Young animals learn to whistle soon after they begin

TABLE 1.—Dates of last capture, with weights, of larger animals in 1948

Date	Weight (g)	Sex
Sep. 29	4000	F
Oct. 4	3700	M
Oct. 7	3600	M
Oct. 8	4000	F
Oct. 29	3500	M

to wander away from the natal den, but do not seem to be capable of making as loud a noise as the adults.

Two observations were noted of a female warning her litter of danger by whistling, the most noteworthy occurring on a May morning in 1948. The female and three young under observation, were attracted by the barking of a pack of feral dogs in the next field. At the first bark of the dogs, the old female immediately stiffened and gave a sharp whistle that sent the young scurrying to the den, followed closely by the female.

LONGEVITY

The oldest woodchuck, *Marmota monax*, lived in the London Zoo for almost 10 years (Flower 1931). Animals up to four years of age were reported at the Rose Lake Wildlife Experiment Station by Linduska (1947a). Six animals were trapped at the Patuxent Refuge in 1947 as adults (two years old) were still alive in 1949 at four years of age. One woodchuck trapped at the Refuge as a yearling in 1947 was still alive in 1952 at six years of age. Hamilton (1934) believes that the natural life span is four or five years. I am of the opinion that the age can be safely extended to five or six years.

FEAR AND DEFENSE

Like most wild animals, the woodchuck will run from a superior adversary. If cornered, however, it is very fierce. Holt (1924) describes an encounter between a wandering woodchuck and a pack of dogs in which the woodchuck defeated the dogs. I have had woodchucks charge me on several occasions but I avoided being bitten by simply stepping aside or putting some object between me and the animal. When a 'chuck has been cornered, he will show his defiance by chattering the incisors. An adult woodchuck can usually take care of

TABLE 2.—Dates of last capture, with weights, of smaller animals in 1948

Date	Weight (g)	Sex
Oct. 13	2400	M
Oct. 13	1550	F
Oct. 15	2800	F
Oct. 22	2050	F
Oct. 29	2400	M
Oct. 31	2300	F
Nov. 3	2600	F
Nov. 6	1800	F
Nov. 11	2550	F

himself against an ordinary-sized dog, but he is no match against an animal as large as a Chesapeake Bay retriever. Dogs running in packs can usually dispatch any woodchuck caught in the open. A pack of feral dogs running on the Refuge in 1949 killed at least six woodchucks and one raccoon in a two weeks period.

MOVEMENTS

Saunders (1922), Gianini (1925) and many others have published notes on tree-climbing woodchucks. It is certainly not a common event to see a 'chuck up a tree, as they are essentially fossorial-terrestrial animals. I have seen three woodchucks in trees during the two years of this investigation.

Woodchucks often live near streams, lakes, and bays, but it is a rare sight to see one swimming. Only on one occasion have I seen a groundhog swim. The animal was released from a box-trap next to a moderate sized creek. Without hesitation, it plunged into the water and swam to the other side. The animal ran along the opposite bank for about 30 feet and then recrossed the creek to a bank den. Numerous citations of swimming woodchucks appear in the literature, among them being Cram (1923), Johnson (1923), and Merriam (1884).

Woodchuck tracks closely resemble those of the raccoon, but can easily be identified by the alternate four-toed tracks of the front feet and the five-toed tracks of the hind foot. The raccoon has five toes on each foot.

Goodwin (1935) states that on more than one occasion he marked a woodchuck as it entered its den in the middle of a field and after carefully plugging all exits, he followed every open leader without success. Apparently the 'chuck was able to dig ahead of the excavator. On the other hand, an old resident of the eastern shore of Maryland told me he had had no difficulty in digging them out of their summer field dens.

HIBERNATION

In Maryland hibernation is progressive, the older and fatter animals go in first, followed by the yearlings and juveniles (tables 1, 2). The same order of precedence holds true as the 'chucks emerge from their winter sleep, the larger ones appearing first. Most of the adults are hibernating by November 1. The last animal to be live-trapped in 1947 was caught on November 13, the last in 1948 on November 11. The first dens found open in 1948 were located on February 16 in a wooded area across the road from the Check Farm. In 1949, the first open den was found on February 15 at the same location.

Numerous records of winter activity appear in the literature. Hall (1930) states that on January 4, 1930 he shot a groundhog near Orton, Ontario. I recorded the probable emergence of a 'chuck on January 11, 1949 at the Refuge. It was the sixth consecutive day of warm sunny weather during which several recent records of high temperatures were broken. A survey was made in the afternoon to see if there had been any interruption of hibernation. Eighteen dens were checked and one on the Conservation Farm had been opened, the unmistakable odor of woodchuck being present. A careful check of the area failed to disclose the actual presence of a groundhog, so it was

assumed that the animal had returned to the hibernation chamber. A substantial insect hatch and the appearance of sprouting skunk cabbage was noted on this date.

I held a woodchuck captive under simulated natural conditions throughout the winter of 1948-49. The animal was placed in the pen on October 12, 1948, and immediately made use of the box provided. The 'chuck, an adult female, remained active throughout October. By November 10, she showed signs of torpor and would remain in the box for several days at a time. The last time the 'chuck was known to be out was on December 5, 24 days after the last animal was observed on study areas. Weekly examinations of the animal were started on January 21, 1949 and continued until the animal emerged from hibernation. Table 3 shows the weekly weight and the differences between the anal temperature and that of the outside air.

It is commonly believed that the woodchuck emerges from hibernation in an emaciated condition. This has not been found true at Patuxent Refuge. Hamilton (1934) gives a weight loss during hibernation of one-third to nearly

TABLE 3.—Weight loss and body-air temperatures of a hibernating woodchuck under simulated natural conditions

Date	Weight (g)	Temperature °C Anal	Air	Remarks
Oct. 12, 1948	3600			Placed in pen on this date.
Jan. 21, 1949	3200	10.8	2.0	Average non-hibernating temperature 37°C
Jan. 28, 1949	3200	11.5	22.0	Claws elongated. Teeth somewhat elongated and covered with yellow deposit.
Feb. 4, 1949	3200	9.0	10.5	
Feb. 11, 1949	3175	8.0	2.0	No visible change in condition.
Feb. 18, 1949	3075	9.5	14.0	
Feb. 25, 1949	3050	10.0	11.5	
Mar. 4, 1949	2925			Animal emerged from from hibernation in last 24 hours. Vulva not enlarged. Teeth and claws quite long.

half of the fall weight. On the Refuge, the weight loss during hibernation of two juvenile and 10 adult tagged animals from October to late February and early March was 30.45 per cent (table 4), somewhat less than Hamilton's estimates. It must be remembered, however, that the winters are more severe in New York than in Maryland, which may account for the difference. All animals handled on the Refuge were in good physical condition upon emergence from hibernation. Weight losses continue into early April and somewhat later for gravid females.

There has been some speculation as to how much mortality occurs during hibernation. An examination of the records of tagged animals at the Refuge indicates that hibernation mortality is negligible, although some undoubtedly occurs. However, hibernation mortality may be an important decimating factor, especially in areas where drainage is poor and there is a scarcity of good hibernating sites. It is possible that disease may also be a factor.

During January-February 1949, a hibernating woodchuck held captive under simulated natural conditions was examined at weekly intervals. The animal was often handled for 15 minute periods before being returned to the box. At no time did the eyes open and the animal could be safely handled with bare hands. The actions exhibited by the woodchuck indicated that any animal hibernating in an open chamber or burrow would be subject to easy predation. The hibernating 'chuck was cold to the touch, showed no signs of normal breathing, and no outward indication of heart beat.

The major causes inducing hibernation and recognized as practically essential by all writers have been summarized by Benedict and Lee (1938) as cold, absence of food, or hunger, darkness, confined air, absence of external stimuli, sleep, season, and many other contributory causes dealing with anatomical, nervous, or endocrine factors. Benedict and Lee have observed that "the normal non-hibernating marmot, with a body temperature of 37° C, has a

TABLE 4.—Weight loss during hibernation

Animal No.	Hibernation		Weight (grams)			
	Last Date Before	First Date After	Before Hibernating	After Hibernating	Loss	% Loss
	(1948)	(1949)				
			Juveniles			
1030-1031	Oct. 22	Mar. 29	2050	1200	850	41.5
1736-1737	Sep. 26	Mar. 25	1900	1575	325	17.1
			Adults			
128	Oct. 8	Mar. 17	4000	2900	1100	27.5
137	Oct. 29	Feb. 19	3500	2550	950	27.1
274-275	Oct. 4	Feb. 25	3700	2100	1600	43.2
1013	Sep. 10	Mar. 15	5000	3200	1800	36.0
1020-1021	Sep. 30	Mar. 15	4000	3100	900	22.5
1108-1109	Oct. 12	Mar. 4	3600	2925	675	18.7
1403-1404	Oct. 14	Mar. 22	4500	2000	2500	55.6
1444-1445	Oct. 25	Mar. 24	3050	2050	1000	32.8
1544-1545	Oct. 7	Feb. 27	3600	2600	1000	27.7
1616-1617	Sep. 29	Mar. 26	4000	3000	1000	25.0

basal metabolism, on any basis of calculation, far lower than any other warm-blooded animals of approximately the same size."

Wade (1950) concludes that frozen soil presents a barrier through which ground squirrels cannot dig their way, thereby holding them imprisoned until sufficient thawing and loosening of the soil makes digging-out possible. In Maryland, frozen soil presents no barrier to a woodchuck's emergence, the amount being insignificant, especially in wooded habitats where the majority of hibernating dens are located.

REPRODUCTION AND GROWTH

Breeding period.—Woodchucks do not commonly breed until they are two years of age. Only one positive and two doubtful records of yearling females having bred have been secured over three breeding seasons. Eighteen yearling females were handled either during or shortly after the breeding season that showed no signs of being or having been in breeding condition. Hamilton (1934) reported yearling females breeding, as did biologists at the Rose Lake Wildlife Experiment Station in Michigan (1940-41). I believe that it is safe to say that no more than 10-25 percent of the yearling females on the Refuge breed, elsewhere the situation may be different. Yearling males showed few indications of being in breeding condition, although it is highly likely that they, like the females, actually were capable of breeding in some cases. On March 29, 1949 a yearling male was captured that showed some scrotal swelling. A smear was taken from the cauda epididymis of the animal. No mature spermatozoa were found. The two testes were about the size of large beans. The animal weighed 1550 grams. Hoyt and Hoyt (1950) report the successful breeding of male and female litter mates as yearlings. Most of the mature animals were in breeding condition several weeks before the yearlings, indicating that the yearlings, when they do breed the first year, do so at a later date.

The males and females often consort together in the breeding season and may remain together for some time. Schoonmaker (1938) notes that as the time for the birth of the young approaches, the female either drives the male from the den or discourages his attentions to the extent that he willingly leaves.

In Maryland, the breeding period of adult animals extends from late February through March. Twichell (1939) reported that in central Missouri the breeding season began during mid-February. Undoubtedly, the season is somewhat later in more northern latitudes.

Before attempting any breeding habits studies, one of the most important things to know is how to distinguish the two sexes. To the unitiated, sex identification of woodchucks may be confusing. Suffice it to say that the penis of the male is about twice as far from the anus as is the vulva of the female. The average length of the perineum of the male is about an inch, the female about half an inch. This will vary with different-sized animals.

Most litters are born around the middle of April in Maryland. The earliest known birth occurred on April 5, 1949. Practically all litters have been born by May 10, indicating a breeding period extending over about four weeks.

Gestation.—Hamilton (1934) reported the gestation period as about four weeks, but based his estimate mostly on circumstantial evidence. My experiments closely substantiate Hamilton's calculations.

The first problem in attempting breeding habits work is to secure a sufficient number of adult females that have not bred. This was accomplished by holding one female over the winter in a pen and trapping three others shortly after they emerged from hibernation. Since adult woodchucks breed soon after emergence, it was necessary to secure adult females as early as possible. Dug-in traps were used with success.

The females were placed in separate holding pens and held at least a week before the breeding experiments started. In case any females had already bred, the gestation period would not then be confused with that of the experimental animals. This later proved to be a wise precaution, as one of the four females was pregnant when placed in the pen.

The breeding experiments were of two types: (1) two females were artificially inseminated; and (2) an adult male was placed in the large pens for a period of 48 hours with each of the other two females.

To secure a supply of mature sperm, a large adult male was killed. Different areas of the reproductive tract were sampled by putting a drop of fluid on a slide and examining it under the microscope. The best sample was obtained from the epididymis. The organ was squeezed and dipped into a normal salt solution. A sample of the solution was checked under the microscope to determine if a sufficient supply of sperm had been obtained. The solution was injected into the vaginas of the two females with a medicine dropper.

In the other breeding experiment a large adult male was placed in the pen with each female and allowed to remain for 48 hours. The same male was used in each case.

Only one of the artificial insemination experiments was successful. One of the females gave birth to a litter two weeks after the experiment started, so, obviously, conception had occurred before the animal was trapped. The artificial insemination experiment started on March 27, 1949. The pens were checked every 24 hours. On April 27, 1949, a litter was discovered, giving a gestation period of 31 or 32 days.

In the pens where the adult male was placed for periods of 48 hours, both experiments were successful. The male was placed in one of the pens on March 26, 1949, and birth occurred on April 28, or during the previous 24 hours, giving a maximum gestation period of 32 days, plus or minus one day. The other experiment ran from March 28 to May 1, giving a gestation period of 33 days, plus or minus one day.

Young per litter.—Records have been compiled on 29 females in Maryland for an average litter of 4.6. Included are embryo counts and examination of placental scars soon after parturition. The largest embryo count obtained was eight. Hamilton (1934) gives the average litter as 4.07 in New York. Howell (1915) notes a litter of nine.

Litters per year.—All available evidence indicates that the woodchuck is monestrous, that is to say has only one estrous cycle or breeding period each year. No record of more than one litter during a year has been recorded.

Development of young.—Four litters, resulting from the breeding experiments, were born in the pens. One litter was killed by the mother shortly after birth. The other three litters were destroyed within 10 days, one by a pack of dogs, the other two by drowning. Apparently it is not an uncommon occurrence for the female of both domestic and wild species to kill her young.

Three litters were examined within 24 hours after birth. Two litters consisted of three young each, the other five.

The average weight of young woodchucks less than 24 hours old was 27.2 g. Of the 11 animals examined six were males and five females.

The young are born blind, almost naked, and quite helpless. The skin has a pink-reddish tinge. The fore legs are much better developed than the hind legs. No teeth are present.

Only three animals from one litter were available for examination at the end of one week. The young ranged in weight at this time from 45-62 g, a male being the largest. The muzzles have a whitish appearance and hairs are beginning to grow, including some of the vibrissae. Other hairs under the eyes are quite long compared to the rest of the body. The navel is well healed at this time. The fore legs continue to be larger and better developed than the hind legs. A slight slit is beginning to form in front of the eyes. Hamilton (1934) gives an excellent account of the development of the young from birth through seven weeks.

In 1947 the first young animal of the year was caught on May 23 by D. L. Allen. It was well developed and capable of living independently. The weight was 450 g. In 1948 the first animal was caught on May 27, weighing 400 g. By July the female apparently tires of their care and the young begin to disperse, usually occupying old abandoned dens.

The nursing period.—During this investigation no males were seen to consort with females after the young were born, although it is not unlikely that it might happen. Pregnant females were commonly caught in box-traps until one or two days before parturition. They would then disappear for about a week. Captive females held in the breeding pens were very belligerent for several days after parturition and refused food during this time. On the third or fourth day they again began to feed and were eating heartily after seven days.

Weights.—Securing the weights of individual animals has played a prominent part throughout the investigation. Weights often varied for the same animal, even on the same day. Woodchucks are notorious eaters, sometimes consuming almost a pound of food at one feeding. Therefore an animal caught soon after the morning meal will weigh considerably more than if the same animal was caught two hours previously. In the long run, however, such differences should be compensated for if enough samples are taken. During the investigation more than 500 weights were secured but only those obtained with an interval of one week are used. Weights were taken to the nearest 25 g. All weights used were obtained on the Refuge. The heaviest animal handled during the investigation on the Refuge weighed 5000 g. Several animals handled on the eastern shore of Maryland weighed 6000 g. Mr. Ray Prettyman, of Galena, Maryland, who has killed about 2000 woodchucks and who is an excellent wildlife observer, recalls that the largest animal he killed weighed 15¼ lbs. or approximately 6900 g. John Webb, of Frankfort, Kentucky, held a woodchuck captive for three years as a pet that weighed 37 lbs. as an adult.

Figure 6 shows the mean weights of an individual obtained in four different seasons, through three different age classes. The weight loss during hibernation is shown in the graph.

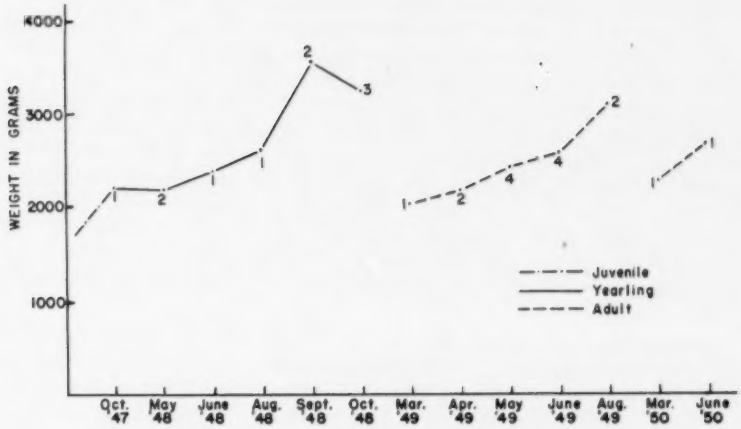

Fig. 6.—Rate of growth of an individual woodchuck (no. 1444-1445). Numerals indicate number of observations

An examination of all weights by sex and age classes shows that in 12 out of 22 cases males averaged greater weights than females, the females showing averages quite a bit higher in September in the yearling and adult age classes.

Figure 7 shows the mean weights of all animals handled on the Refuge by age classes. Various authors have used the weights of animals as a criteria for aging animals. Such a system was used during this study. Admittedly the use

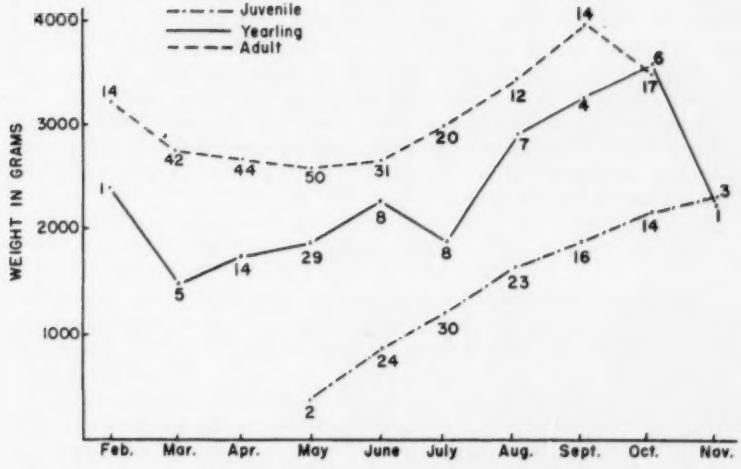

Fig. 7.—Weights of woodchucks in three age classes. Numerals indicate number of observations

of weights will at times lead to errors. However, it is believed that the system is a practical one, in spite of its shortcomings. It is easy to follow and, most important of all, can be applied to live animals in the field. Hamilton (1934) worked out a system of aging woodchucks by less than one year, or more than one year classes by skull and bone measurements. Other methods of aging the animals were tried during the investigation but none proved successful. Ear and right hind foot measurements were taken of a number of live animals, but the records were not consistent, due mainly to the struggles of the animals while being measured. It is entirely possible that a practical system using ear and foot lengths might be worked out if two people were available for field work, or if the animals were anesthetized. Obviously, in using weight as an age criteria, the investigator should make sure he is handling a healthy individual.

Contrary to some reports, the woodchuck emerges from hibernation in a moderately good condition. For the first two weeks after emerging the animal eats very little. Figure 7 shows a drop in weights in the fall that at first glance is puzzling. The reason for this is that the large fat animals are the first ones to go into hibernation (table 1). The 'chucks that have not stored up a good supply of fat remain active until the first hard freeze, then, they too seek shelter from the long winter ahead.

SEX AND AGE RATIOS

An examination of the records made during the investigation reveals that the sexes are distributed almost evenly, there being 103 males to 100 females. The male appears to be promiscuous in its breeding habits.

Age ratios will vary from year to year, according to the success of the breeding season and the presence or absence of favorable climatic conditions. A large number of juveniles were handled in 1948. Again in 1949 a large number of yearlings were trapped, reflected from the previous year's juvenile crop. Trapping records usually showed a preponderance of adults, except in the summer, when the juvenile crop put in its appearance. A substantial number of breeding animals were thus present on the Refuge each year. The reason for the large juvenile crop in 1948 is not easily explained. We do know, however, that in wild animal populations there are ups and downs in the breeding success, sometimes reflected in cycles. There is no evidence available that the woodchuck is a cyclic species.

POPULATIONS

Populations on the two farms appear to be rather stable at the present time. With the continued improvement of agricultural practices on the Conservation Farm, it is likely that some increase of woodchucks will follow. Populations also seem to be rather stable on the Refuge as a whole. Private holdings for several miles outside the Refuge contain few woodchucks. The nearest area in private ownership containing a substantial population was a large farm about eight miles east of the Refuge. One 20 acre field on the farm contained approximately 15 animals. Populations on the two farms at the Refuge varied of course from season to season, and slightly, from year to year. However,

the average total fall population on the Check Farm was about 12 animals and that of the Conservation Farm about 33 animals.

Howard R. Zeller, Wildlife Field Superintendent for the northern part of eastern Maryland, and I have had a 22 acre alfalfa field in Kent County under observation for three years. The populations that this field have produced are remarkable. In the field itself, there have been about 24 active dens for the past three years, in spite of two gassings, numerous hunts, and killings by a Chesapeake Bay retriever. In the summer of 1949 a group of hunters claimed they killed almost 100 woodchucks in the field. Certainly the field itself did not produce that many 'chucks but the habitat was so favorable that other animals moved in from an adjacent area as fast as other animals were taken off. The population of the field and adjacent terrace was not at any time more than 60 animals, including young.

Indications are that the southern woodchuck is increasing throughout most of its range. Bradt (1946) states that woodchucks in Michigan are thought to be making a comeback in numbers compared to their scarcity in the late thirties. Mohr (1947) notes that in Illinois the groundhog appears to be on the increase in many parts of the state, but the increase is not general.

Linduska (1947b) reports populations for the entire area of the Rose Lake Wildlife Experiment Station in Michigan at about three animals of all ages per 100 acres. The population density in some situations was probably as high as 25-30 individuals per 100 acres.

An extensive survey of woodchuck populations was made around Ann Arbor, Michigan in 1950. No areas were noted that compare with those in eastern Maryland. In some places the populations will run 15-20 individuals per 100 acres. Other localities contained few or none of the animals.

Throughout a large area in the vicinity of Ithaca, New York, Hamilton (1934) estimated about five rufescent woodchucks to the acre, with one three acre field containing 30 separate dens.

Census methods.—A reliable estimate of the populations on the two farms was obtained by counting woodchuck burrows, live-trapping, and sight records.

The method described by Burt (1948) was found unsatisfactory as far as the woodchuck is concerned in Maryland. It is possible that a somewhat similar method may be used by first tagging a large number of animals and then, by hunting, arriving at a proportion by comparing the number of tagged to untagged animals after the manner of Allen (1938), who successfully used the tag-kill method in studying rabbits in Michigan.

The most satisfactory censusing method in my experience is to examine an area for active dens. I have found that an average of 75 percent of the active dens actually contain an animal. The figure should be a good index to use in Maryland and the immediate vicinity, elsewhere the situation might be different. There are several discrepancies that may appear if the method is used. One is the difficulty of locating dens in brushy areas, especially during the last half of the summer when vegetation is dense. If all the active dens on an area are located and that information correlated with several days observations to determine just what dens are actually occupied, a satisfactory approximation of

the actual population could be obtained. Such a method is most feasible in pastures that may be surveyed from good observation points.

FOOD HABITS

Hamilton (1934) Twichell (1939), and Gianini (1925) have reported on the food habits of the woodchuck.

Notes on file at the Patuxent Research Refuge pertaining to food habits of the woodchuck indicate that the animals eat the leaves, twigs, and fruit of the apple, peas, beans, carrots, cabbage, celery, pumpkin, squash, potato vines, young plants and roasting ears of corn, vetch, stonecrop, sedges, blackberry, serviceberry, roses, sunflower, and dandelions.

Soybeans, alfalfa, and clover were among the favorite foods as well as furnishing the most desirable habitats. It was interesting to follow the main woodchuck concentrations around from year to year in order to examine what crops they liked best. Of the crops planted on the Refuge farms they preferred soybeans, a hay mixture of grasses and legumes, and corn in that order. Only on one occasion was a woodchuck den found in a wheat field, although they had been in the same field in considerable numbers the previous year when a soybean crop covered the area.

A common complaint against the groundhog has to do with its garden depredations. One or two animals can literally ruin a small garden almost over night. About $25.00 damage was caused by one or two animals in a small garden on the Check Farm in less than a week.

In the summer of 1948, three woodchuck dens in a corn field were under constant observation to determine if their occupants caused crop damage. With one or two minor exceptions, little damage was noted until a heavy rainstorm blew over many of the corn stalks and made the ears readily available.

An examination of 32 stomachs collected in the spring and summer of 1949 indicates that red clover, white clover, grass, chickweed, and alfalfa were the foods eaten most and in the largest amounts. A total of 24 different items were recorded indicating a wide variety of choice at times. The chickweed figured in the early spring foods when there was an abundance of the plants, and probably constitutes one of the main sources of food when the animals start feeding in March, after their emergence from hibernation.

The water requirements of woodchucks are normally satisfied by dew and succulent vegetation, however, the animals will, upon occasion, drink free water.

MORTALITY FACTORS

Hamilton (1934) reports that no one definite factor tending to decimate the woodchuck population and to leave them a weak remnant of their former abundance has yet been noticed to his satisfaction in ten successive years' observation about central New York. According to old woodchuck hunters in Maryland, several of whom are very good observers of wildlife conditions, the woodchuck has been increasing and spreading for 30 years, with no real lapses or periods of scarcity.

Activities of man.—In areas where the habitat is favorable, such as in

dairying or stock raising localities in the East, where alfalfa, soybeans, and clover are principal crops, the activities of man must play an important part in order to hold the woodchuck population in check. The gun, trap, and various forms of gas are used to keep the animals under control.

Several hunters, with the proper equipment, can hold down populations in small areas. The farm boy, with his .22 rifle, also exerts a considerable influence.

Trapping is a method used by many landowners to hold woodchucks in check. Steel traps are the most commonly used, but the smaller ones are not entirely successful because of the woodchuck's strength. For satisfactory results a double-spring no. 2 trap should be used.

Flooding.—The role of water as a mortality factor plays an important part in areas subjected to periodic flooding or in localities where the land is flat, with poor drainage. Even in some areas where periodic flooding occurs, the woodchuck seems to be able to maintain itself. A small hammock in the flood plain of the Patuxent River near the Refuge was under observation for two years. A small woodchuck population maintained itself in spite of at least two floodings.

The woodchuck seems to be the most vulnerable from floodings during the hibernating period. Any animals not holed up in well drained soil during the winter would almost certainly drown. However, the woodchuck apparently has the innate ability to choose favorable hibernation places when they are available.

Flooding during the time the young are helpless in the burrows may occasionally be a serious decimating factor. Heavy rains accounted for the loss of two litters during the spring of 1949, when breeding experiments were being conducted at the Refuge.

Yeager and Anderson (1944) record an interesting experience concerning mortality during a flood in central Illinois. Seventeen dead woodchucks were noted in November, the first dead animal being located about two weeks after the first crest. Circumstances indicate that the woodchucks were driven from their dens in numbers, probably during hibernation, by the rising water and that, unable to find suitable unused dens or to dig others, they died primarily from exposure.

Currier (1949) reports that after two severe floodings of 24 dens, only seven were abandoned. He noted no mortality of adults, but believed many young animals died in the burrows.

Disease.—I have been unable to find any reference in the literature to epizootic diseases having ever caused a decline in woodchuck populations. Undoubtedly diseases do occur in the animals, as in most all living matter, but they do not seem to be an important factor in their population dynamics.

Schoening (1942) lists the woodchuck in records of animals that have been known to be infected with rabies.

Hamilton (1934) notes that tularemia, or rabbit fever, is a debilitating and often fatal disease, which in some cases, is transmitted from woodchucks, rabbits, and other species to man by the wood tick. It is doubtful, however, that many of the fatal cases in man have originated from the woodchuck.

Dr. Don R. Coburn has furnished me with information that woodchucks

suffer from a malady resembling encephalitis. The cause of the disease has not yet been determined. The symptoms are general loss of muscular control with a jerky motion of the head. The animal has difficulty standing and is almost constantly wiggling or shaking. Woodchucks having the symptoms of the disease have been noted two times at the Patuxent Research Refuge, once by me and another time by William and Lucille Stickel. A woodchuck received by Dr. Coburn from the Ohio Cooperative Wildlife Research Unit in 1948 had the symptoms of the disease. Dr. Eugene Dustman of the Ohio Unit has informed me that another outbreak of the disease occurred during the summer of 1950 in that state.

Rocky Mountain spotted fever is probably transmitted at times from the woodchuck to man by the tick.

An interesting case of a mange-like disease was recorded at the Refuge in 1947-48. The disease involved an adult female. A skin scraping was examined by Dr. Coburn but no mange mites were found. During 1947 the woodchuck was in poor shape due to the disease. Although an adult animal, she weighed only 1900 g on April 20, 1948 and bore no litter that year. In July 1948 the animal showed definite signs of improvement. The hair growth was good in the mange-like areas and weight increased considerably. When last handled in 1948 on October 8, she weighed 4000 g. In late 1947 the woodchuck was handled practically every day; probably due to her poor condition she found the trap bait the easiest food to secure. During 1948 the animal was handled only 11 times compared to 39 times in 1947. In 1949 the woodchuck emerged from hibernation in good condition, was placed in a breeding pen, had a litter, and was killed by a pack of dogs a short time later.

Parasites.—The woodchuck handled in these studies were comparatively free of parasites, both externally and internally. In only two stomachs out of more than 40 examined were parasites found, these being the roundworm *Obeliscoides cuniculi*. Twichell (1939), Rausch and Tiner (1946), and Wallace (1942) all note that the roundworm was found in various numbers in specimens they examined. Hamilton (1930) found a woodchuck with the stomach nearly full of roundworms.

A woodchuck was initially tagged in 1947 and listed as a young animal. It was again captured on April 14, 1949, at which time it was a two year old animal or an adult. When caught in 1949 the woodchuck weighed only 1475 g, which is at least 500 g underweight. Figure 8 shows several areas of the animal's body that were hairless with flaky skin and scabs. The 'chuck had apparently scratched herself in an attempt to rid the skin of mites that were literally swarming over the body. The entire outer surface of the body was covered with flakes of skin due to the irritation of the mites. A number of mites were preserved and identified by Dr. E. W. Baker of the U.S. National Museum as the parasitic mite *Atricholaelaps glasgowi* (Ewing) in the family Laelaptidae.

On February 15, 1951 James Linder found a woodchuck wandering aimlessly around in the snow near Ann Arbor, Michigan. The date on which the animal was found is several weeks before the usual time of emergence from hibernation. A laboratory examination showed that the animal was greatly emaciated, was heavily parasitized with mites, and had numerous masses of

Fig. 8.—Scabby area caused by mites and scratching

necrotic tissue covering most of the body and head. The mites were identified by Dr. Baker of the U.S. National Museum as *Haemolaelaps glasgowi* (Ewing), family Laelaptidae. He noted the mites were parasitic and are found on numerous small animals throughout the country. The necrotic tissue was evidently a secondary infection associated with the mites. The tissue consisted of a whitish cheesy substance and covered areas as large as 20 mm in diameter. No culture were made of the infected tissue but the lesions closely resembled those of Schmorl's disease in rabbits.

The common wood or dog tick usually appears in April, increases in abundance during May, and reaches a peak in late June and July. They taper off abruptly in August. A few are still seen in September and rarely in October. Ticks have been observed on raccoons and skunks throughout the year. None of the woodchucks, examined shortly after emerging from hibernation, was infested with ticks but ticks have occasionally been found on animals shortly before they hibernated in the fall.

On several occasions I noted the presence of tumor-like spots on woodchucks caused by the larvae of parasitic Diptera.

The woodchuck often serves as host for fleas, but not in as large infestations as are often found on many other animals.

Predators.—Undoubtedly predation is an important factor in woodchuck mortality. Foxes and dogs are the two most serious predators, but other animals such as badgers, snakes, bears, hawks, and owls will take woodchucks at times. Bears, dogs, and foxes have been known to dig woodchucks from their burrows. Predation in this manner is probably not serious due to the woodchuck's digging ability when he is awake, and the fact that most of the hibernation chambers are plugged, making discovery difficult.

Beule (1940) reports that black bears have been known to dig woodchucks out in the fall and early spring when other food was scarce. In another case, Beule reported that a young woodchuck was found in the stomach of a large

rattlesnake, and noted sight records of red-tailed and red-shouldered hawks being seen at fresh woodchuck kills.

Predation by the fox is confined mostly to young animals. The older woodchucks are able to defend themselves quite capably against a single animal. At the Refuge, feral dogs were found to be the most serious predators. The animals usually ran in packs of from two to six. On two occasions the trap line had to be closed down because the dogs had become so proficient in locating the animals in the traps. A large woodchuck is often able to defend himself against a small or medium-sized dog but is no match for larger ones. Feral dogs on the Refuge often caught woodchucks, raccoons, and skunks in the open fields and dispatched them with ease. At least 15 woodchucks were known to have been killed by dogs in the summers of 1947, 1948, and 1949. Individual house dogs often become excellent woodchuck hunters.

Other mortality factors.—As with all living things old age takes its toll, although many wild animals succumb to predation, accidents, or disease before they become senile. In May 1948, an aged adult female 'chuck was turned over to Dr. Don R. Coburn for examination. The animal showed great emaciation. There was no evidence of bacterial infection or specific organic disease. The condition of the molar teeth was indicative of advanced age and may have accounted for inadequate mastication of food and a condition of inanition.

Leedy (1949) noted that woodchucks were apparently able to survive a hot fire that burned over a 100 acre area. The dens probably served as refuge areas for woodchucks and other forms of wildlife. About one-third of the dens had been reopened after the fire and some woodchucks were travelling a distance of 75 yards to obtain food.

DEN STUDIES

Woodchuck dens are not hard to recognize if carefully examined. They may at times be confused with fox, skunk, and badger burrows but in each case there is usually some evidence indicating that the occupant is one or the other of the animals.

The den of the groundhog has from one to five entrances. It is almost always located in well drained soil, and can be recognized by the mound of fresh soil at the entrance, often a plunge hole, and numerous trails leading from the den entrance to feeding areas. Usually, several times a week, the woodchuck will clean out the burrows and deposit fresh soil at the main entrance. No other animals are known to do this regularly. Occasionally the musky odor secreted by the anal glands of the woodchuck will identify the occupant of the burrow.

When foxes appropriate woodchuck dens for their own use there is an absence of fresh soil about the entrance and animal remains will usually be found at the den.

Badger dens are quite similar to those of the woodchuck but the flat-bodied animal generally constructs a burrow that is wider in a horizontal plane than that of the woodchuck and again is lacking the mound of freshly deposited soil.

General construction.—Merriam (1884) speaks of two different types of entrances, one dropping abruptly downward, the other at a moderate angle. The main entrance usually has the characteristic mound of fresh soil. The plunge hole is excavated by burrowing up from one of the main galleries, leaving little, if any soil on the outside. It is often located on an almost vertical plane and serves as a well concealed escape route into which the animal can disappear very rapidly. At times, woodchuck dens will be found that are lacking the usual mound of soil. Many of the dens showing this characteristic are old dens that have been reoccupied. Any cleaning out of material from new diggings is probably pushed into one of the old chambers instead of being brought to the surface. The plunge hole is almost always considerably smaller than the main entrance, averaging about six inches in diameter but often even smaller.

Woodchuck dens may be roughly classified under two broad classifications: one located in wooded or brushy habitats and often on sloping ground, the other in open situations in flat or gently rolling topography. The former usually serves for hibernating purposes but may be used throughout the year. The latter den is occupied only in the late spring, summer, and early fall. A den located on steep or moderately rolling ground in wooded habitats usually has less entrances than one in open situations. Frequently, burrows situated on terraces had only one entrance, seldom more than two. Dens located in open territory varied in the number of entrances from one to five.

A survey of dens on the two farms at the Refuge showed that the diameter of the main entrance taken one foot beneath the ground level varied from five to 16 inches, the average being 10 inches. The slope on which the burrows were located varied from level to those that were almost vertical, but all were situated in gently rolling country. The average number of entrances was 1.8. Of the 39 dens surveyed, 18 had one entrance, 15 had 2, 4 had 3, one had four and one 5.

The actual construction of dens differs considerably. One den that was excavated during the investigation had only one simple burrow, running in about five feet from a terrace, and terminating in a nest chamber. Another den, had five entrances and consisted of a veritable maze of burrows, blind chambers, and four nests. The den was evidently several years old and from time to time had been enlarged by several succeeding generations of groundhogs. The main entrance varies in its slope according to the slope of the ground in the immediate vicinity. In dens constructed on level or near level ground the main entrance slopes at a moderate angle for three or four feet. At the bottom of the main entrance is usually a large chamber or turn around area and from there the burrow may assume diverse forms. In most cases the burrow inclines slightly upward after reaching the lowest point and continues its climb, terminating in several branches, one of which serves as the nest chamber. The other branches are often either blind passages or serve as chambers for the deposition of fecal remains. At other dens, the main entrance will level off after the initial dip from the ground surface, and then either incline upward into a nest chamber and other branches or incline downward again for some distance before terminating in the end chambers. In most all cases the nest chamber is constructed on a higher plane than the deepest part of the burrow system. Merriam (1884) notes that he discovered one nest

chamber that was within a foot and a half of the ground surface. Two similar nest chambers were excavated during this investigation.

In dens located on steep slopes, the type of burrow system is quite different from those located on level or near level ground. One den located on a terrace actually sloped upward for the whole distance, terminating after about eight feet into two branches, one a nest chamber, the other a fecal chamber. Another terrace den sloped downward for several feet and then inclined upward for the remainder of the distance, finally terminating into three branches.

The plunge hole, previously referred to, usually descends at a vertical or near vertical angle from the ground surface and may termniate, after a two or three foot drop, in a turn-around chamber. Sometimes the end of the plunge tunnel will level off after dropping a foot or two below the ground surface and then by a slight incline connect with one of the burrows, often the main one.

The nest chambers were generally located at the end of burrows, but not always. Nests were found at all levels and in all parts of the burrow system, except within a few feet of the main entrance. The nests consist of dried and shredded leaf material. In several cases dens were excavated that contained nest chambers that were bare of any leafy material, the woodchuck probably being content with the bare soil as a resting place.

An average den drops from three to four feet below the level of the ground surface, although some go considerably deeper. The deepest den investigated was slightly over five feet in depth. Two dens located along a brook on the Check Farm dropped only two feet in one case and two and a half feet in the other. The largest den excavated had five entrances and had a total of 42 feet or more of tunnels. Nests were found at three different locations in the large den.

Hamilton (1934) notes that excrement is seldom encountered about the den, it being deposited usually in a dry chamber within the burrow or buried in the mound at the entrance hole. Excavations made during the present study thoroughly substantiate these findings.

Hibernation dens.—The location of hibernation dens differs markedly from those found in open hay, pasture, and crop fields in the summer. Without exception, all dens known to contain hibernating animals were located either in wooded or brushy habitats on well drained sites.

A well drained locust knoll on the Woodward Estate near Bowie, Maryland was closely watched in the spring of 1948 and 1949 and found to be a veritable heaven for hibernating 'chucks. At least 20 animals were recorded on the area in the early spring of 1949.

Hamilton (1934) and Allen and Shapton (1942) both indicate that the suspected hibernation chamber within the burrow of the woodchuck is often plugged off from the main passages.

Excavations conducted during this investigation further substantiated the theory that woodchucks hibernated in plugged-off chambers. A total of 22 dens were excavated on the Refuge in 1947-48. Only one hibernating animal was recovered, and then only after a bulldozer was called in to pull up a tree. All open tunnels were excavated with shovels. One loosely plugged tunnel was followed until it ran into a maze of tree roots. The tree was pulled up

and there the animal was, safely protected from predators and the elements. (See Den Studies.)

Summer dens.—As soon as the hay, pasture, and crop fields begin to turn green, many woodchucks desert their well protected winter dens and move into the crop areas where their every want and need is within a few feet of the den entrance. If well drained locations are available, they will usually select them in preference to sites that might easily be flooded. However, their judgment (if they actually have any) is often poor. Four different den sites were known to have filled with water, one of which had a recently born litter that probably drowned. All the adult animals survived, simply moving to more favorable locations. Two of the water filled dens were later reoccupied, one by a previous occupant. Where the habitat is favorable, many animals prefer to locate their dens around the edge of fields and feed out into them from the den location. Such dens are easily located by the trails leading from the den.

Woodchucks show a definite liking for certain fields and shun others. Soybean, clover, alfalfa, clover-grass, and corn fields are preferred. Wheat and other grain fields are seldom used. After the growing season has progressed, woodchuck dens are difficult to locate, the investigator often stepping on them before they are sighted. Fields containing dense vegetation offer extremely good protection, except when they are mowed.

Woodchucks begin moving into the field dens about a month after they emerge from hibernation and they reverse the process when preparing for their winter sleep, abandoning the field dens about a month prior to their disappearance into the ground. In Maryland the field or summer dens are in general use through the months of April, May, June, July, August, and September. April and September are border months, during which the movement to and from the dens is in progress.

Winter den studies.—During the winters of 1947-48 and 1948-49, an intensive program of den studies was carried out. In the fall months preceding the hibernation period, the movement of woodchucks from the summer dens to the hibernating dens was followed. Again in the spring, when the woodchucks began emerging from hibernation, all known dens were watched in order to check their use during the winter. One of the best ways to check a woodchuck den in the early spring is to examine all sapling trees within 15 feet of newly opened dens. If there are fresh tooth marks, it is more than likely that a woodchuck has used the den for hibernating, especially if the den is in a wooded area. Why woodchucks chew on trees is not exactly known. The most plausible explanation is that they need to wear back their incisors and exercise their jaw muscles. The material that is eaten might also serve the purpose of putting the alimentary tract back into a functioning condition.

Fisher (1893) carried on a series of den studies during the summer and published an excellent summary of his findings. In the present studies, an intensive program of den excavation was carried out on the Refuge. During the fall of 1947 the movements of woodchucks were closely followed, although very few were caught after they had abandoned their field dens. The locations of all dens known to be used by woodchucks were spotted on a map, including both field dens and those located along banks, brooks, and woodland borders.

It was assumed that during January woodchucks would be in deep hibernation and, consequently, that would be the best time to dig them out.

Fourteen dens were excavated in 1947-48, from which only one woodchuck was recovered. Habitats of wide variety were selected to check the accuracy of reports that woodchucks moved into wooded areas during hibernation.

Two hibernating jumping mice, *Zapus hudsonicus*, were found in woodchuck dens on January 7-8, 1948 (Grizzell 1949a).

On January 20, 1948 a den was excavated in a wooded area near the border of the Conservation Farm. After finding the summer or fall nest chambers, about six feet from the main entrance, a narrow, partly filled-in burrow was discovered. The tunnel was followed with some difficulty and only by probing with the hand could the burrow be found at times. The tunnel contained considerable soil. Apparently the 'chuck had packed the soil behind as he dug in for the winter. When the burrow approached a tree and started under the roots, the direction was lost. A tractor was obtained and after the tree had been pulled from the soil, a woodchuck's head emerged through the loose dirt. After some pictures were made, the animal was removed and the nest chamber excavated. The 'chuck was awake when first observed but was very sluggish and easy to handle. The nesting material consisted of partly rotten and well-chewed leaves. It is possible that our digging, the noise of the tractor, and the shock of having a tree jerked out from over his head may have aroused the animal. At the time of the excavation the temperature was about 34° F, with a low of 15° the previous night. There was some snow on the ground and the soil was frozen about six inches deep. Figure 9 shows a diagram of the excavated den.

During the months of February and March 1948, a close watch was maintained on all dens previously excavated in January. Of the 13 dens excavated, but apparently lacking woodchucks, three were subsequently found to contain hibernating animals. All dens excavated were examined for blind burrows and chambers, but apparently the woodchuck is so skillful in hiding his hibernation chamber location that it would take several days of probing and digging to find the animal. After the resident animals had excavated the blind burrows, they were dug out to determine their location and position.

It was found during the excavation work that, when possible, the woodchuck will locate the hibernation den under the roots of a tree or stump. Such a location gives maximum protection from predators and seeping water. During February and March, a survey was made of the two farm areas to determine the location of hibernation dens not previously located during the fall. All hibernation dens found were in wooded areas near field borders, most of them on sloping ground.

During late January and early February 1949, woodchuck den excavations were carried on as weather permitted. Eight dens were excavated. Instead of just opening the main burrows of one den after another, two of the most likely occupied dens were excavated on all sides after the main burrows had been dug out. At both of the dens, blind runways and chambers were found that were not directly connected with the main systems. In spite of the additional diggings no hibernating woodchucks were found in any of the eight dens excavated.

One den produced a variety of fauna. A rabbit, dead not more than one

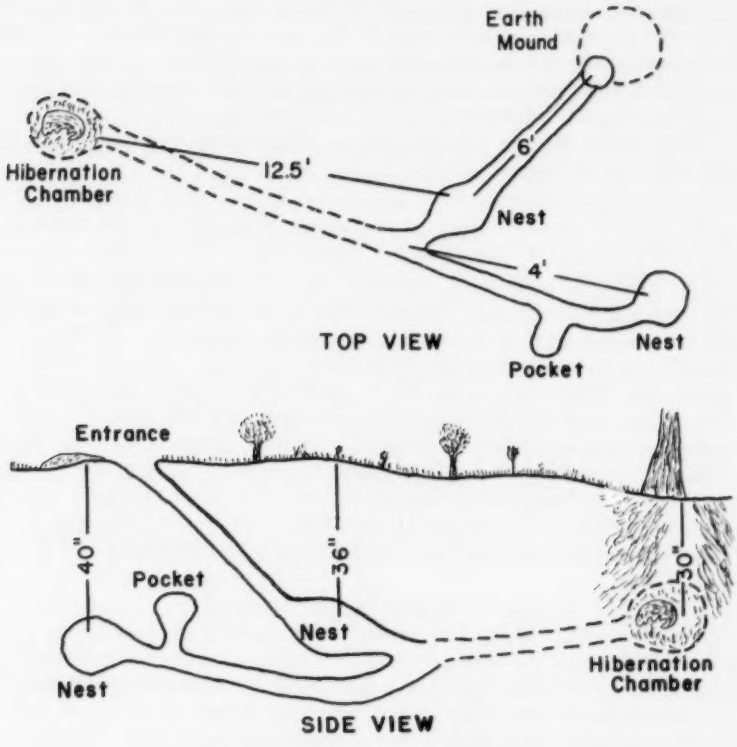

Fig. 9.—Diagram of an excavated den

or two weeks, was found about four feet in from the entrance of the burrow. Three snakes and a salamander were found in the surrounding soil (Grizzell 1949b). A short-tailed shrew, *Blarina brevicauda,* was also found that had been feeding on the flesh of the dead rabbit.

The opened dens were checked periodically as the woodchuck began emerging from hibernation in the spring. A final check on April 10, 1949 indicated that two of the eight dens excavated had contained woodchucks during the hibernation period. The animals had secreted themselves so well that their hibernating location was not found.

Den sites.—Moss (1940) Anderson (1949) and biologists at the Rose Lake Wildlife Experiment Station (1940-41) have found that the woodchuck is partial to certain soil types, mainly loams and sandy loams. Woodchucks were widely selective in the choice of soil types for summer dens at the Refuge but showed a definite liking for the sandy loams, followed by the silt loams, loams, and loamy sands in that order.

Soil types did not seem to have much influence in selection of winter den sites. A well drained and protected situation seemed to be more important.

Land use and cultural practices were factors that definitely influenced the selection of summer den sites, provided the area was well drained. A pattern of movement from one year to the next according to the cultural practices was evident. On the two farms soybean and hay crops were the favorites and could be expected to contain a number of dens each year.

The percent of slope and the exposure did not seem to be important considerations in the location of dens.

HABITAT RELATIONSHIPS

As with many other wild animals, such as the whitetailed deer, the cottontail, and the bobwhite, the coming of civilization and its attendant cultural practices have tended to increase the woodchuck populations. Formerly, the woodchuck was confined to forests and forest openings. As the country was opened and planted to clover, alfalfa, and other hay crops, the woodchuck moved from its former forest home into the more favorable farmlands. Small populations are still found in forested areas some distance from the nearest farm, but generally the woodchuck seems to prefer a combination of wooded areas and open fields, using the wooded areas for hibernation sites and the fields for feeding. The open areas are utilized only in the summer and even then the woodchuck shows little inclination to get too far from a wooded site.

ASSOCIATED SPECIES

In considering the ecology of the woodchuck, as related to associated species, wildlife workers have long maintained that the animal is unique in contributing to the survival of a number of other animals.

The cottontail rabbit occupies the most important place in any consideration of the value of woodchucks. The rabbit is not capable of digging extensive burrow systems but readily takes over the dens that woodchucks have provided. The groundhog is in deep hibernation when the rabbit has the greatest need for the burrows so no interspecific competition is apparent.

Clean farming is the vogue in many parts of the country at the present time. As fence rows, brush piles, rock piles, and other odd areas are removed to make more room for the cash crops, the rabbit becomes more and more dependent upon the woodchuck burrow in the winter, both to escape its many enemies and provide a place of protection from frigid temperatures and winds.

Other animals beside the cottontail also depend on the dens constructed by woodchucks at one time or another. The skunk, an important furbearer, dens up in woodchuck burrows in cold weather. Foxes appropriate groundhog burrows in the spring for use as natal dens. The opossum and raccoon will often use burrows when old logs or den trees are scarce. Many animals will take advantage of the nearest burrow when closely pursued by either natural enemies or hunters. Chipmunks, ground squirrels, weasels, and various species of mice, all important in the ecology of an area, often take advantage of the retreats provided by the woodchucks.

Rabbit.—Petrides (1942), Beule (1940), Linduska (1947b), and Gerstell

(1939) have reported on the ecological relationship of the woodchuck and the cottontail.

My observations and field work substantiate the work of the previous authors. Under light to moderate wind conditions and temperatures above 30° F the use of burrows by rabbits was found to be slight. There was moderate use of holes when the temperature varied between 20 and 30° F and heavy use of dens below 20°, especially if strong winds were evident.

Temperatures taken with maximum-minimum recording thermometers in woodchuck dens and in the nearest location likely to harbor a rabbit revealed, that even during severe winter weather for that region, the temperatures of woodchuck burrows at no time fell below 31° F. The thermometers were placed as far down the burrows as possible, usually five or six feet.

Skunk.—In spite of its well deserved reputation as a *stinker*, the eastern skunk is an important furbearer and a common farm animal. Its well known tendency to appropriate various nooks and crannies for shelter and rearing purposes is common knowledge. The skunk will readily take over an old wood pile, a former woodchuck den under farm buildings, or woodchuck burrows in fields or wooded areas. Allen and Shapton (1942) found five skunks in 36 field dens that were excavated in Michigan.

No skunks were dug out of the 22 dens excavated on the Refuge, however skunks were often live-trapped at den locations and when released they would return quickly to the burrow.

Not only do skunks use woodchuck dens for shelter in the winter but often make use of them to rear their families. On several occasions I caught small skunks at woodchuck dens. In the spring of 1949, three small skunks were caught at the same time in a box-trap next to a woodchuck den. When released they scurried into the burrow.

Opossum.—Somewhat like the skunk, the opossum will use any vacant woodchuck den, woodpile, hollow tree, old building, or odd area that is convenient. Opossums will use woodchuck dens both as refuge from their enemies and as a cozy retreat during severe winters. Often abandoned dens will be used as natal dens in the spring. The marsupials were caught on several occasions at woodchuck dens in the spring while nursing young.

Fox.—While studying the red fox in Michigan I found that most of the natal dens used by foxes were actually woodchuck dens that had been further excavated. The majority of the fox dens were found in brushy or wooded areas. Seagears (1945) mentions that most natal fox dens are revamped woodchuck dens.

Whether or not foxes will actually drive out a woodchuck and take over a den has not actually been determined. It is doubtful that this often occurs, however, as dens are usually selected by foxes for natal purposes before the woodchuck emerges from hibernation.

Raccoon.—Stuewer (1943) notes that if the raccoon's favorite tree den is not available, a home is made in a fallen log, a crevice of rocky outcroppings, or in a ground den. Robert T. Butterfield, formerly Leader of Ohio-F.A. 14-R (Testing methods of increasing raccoon populations) has furnished some interesting information of the relationships between the woodchuck and raccoon

(personal communication). A total of 319 animals were followed to refuge spots after being released from livetraps with 46 percent choosing ground dens as against 38 percent seeking refuge in various kinds of trees. The animals were not too closely pressed and were often followed for several miles before they sought refuge. Nine separate raccoons were recorded as having taken refuge in one series of ground dens in four years of trapping. Butterfield set traps at the series of ground dens previously mentioned, fixing them so that whatever was in the den would have to enter the trap. In two cases raccoons were captured.

Good raccoon populations have often been found where there is an actual scarcity of good den trees. Butterfield live-trapped 97 raccoons on a 2400 acre area that had only five natural tree dens, but lots of ground dens and rock bluffs.

Another observation by Butterfield indicates that on occasions there may exist interspecific competition for ground dens between woodchucks and raccoons, especially if there is a scarcity of natural tree dens. He observed a woodchuck and a raccoon emerging from a ground den in a fierce struggle. Shortly thereafter, he caught a badly mauled groundhog at the same den.

As far as I have been able to determine, the literature does not mention raccoons using woodchuck dens for breeding purposes. Butterfield's observations in Ohio, although not conclusive, indicate that ground dens may be used for natal purposes by raccoons. He has records of several young animals being caught at ground dens, and when liberated, going into a groundhog den. On one occasion, two young animals took identical routes. Another observation noted a nursing female captured at a groundhog hole, and when released from a distance of 20 feet, going directly into the den.

Other animals.—Apparently most all small and medium-sized mammals will, at times, use woodchuck dens. On one occasion two wood mice were caught in a trap next to a woodchuck den. When released, both animals quickly ran into the burrow and disappeared. On another occasion a gray squirrel was livetrapped and released near a woodchuck den. The animal immediately went into the woodchuck den, in spite of the fact that a tree was next to the burrow and many more were in the vicinity. I waited fully five minutes but the squirrel failed to reappear.

Birds, especially quail, pheasants, and ruffed grouse, have at times been observed using woodchuck dens.

Liers (1951) notes that the river otter (*Lutra canadensis*) uses the burrows made by other animals as natal dens. Two different litters were observed at former woodchuck burrows, one 150 yards from water, the other about half a mile.

Other animals that have been observed using woodchuck dens are jumping mice (*Zapus hudsonius*), chipmunks (*Tamais striatus*), meadow voles (*Microtus pennsylvanicus*), short-tailed shrews (*Blarina brevicauda*), house mice (*Mus musculus*), white-footed mice (*Peromyscus leucopus noveboracensis*), pine voles (*Pitymys pinetorum scalopsoides*), and several species of snakes.

RANGE AND MOVEMENTS

The ranges and movements of woodchucks vary widely under different

conditions. Home ranges often depend on the closeness of a good food supply and the amount of protection afforded by the habitat. Seasonal movements may be dictated by juxtaposition of summer and winter requirements for food, habitat, and density of animal populations during the breeding season.

Home ranges.—Rall' (1945), working with marmots (*Marmota baibacina* Kastsch) in the Central Tyan-Shan region of Russia, has observed that in the steppe-plain type, where the burrows are not numerous and are distributed evenly, the animals make long journeys of up to 400 meters. In colonies of the ribbon-ravine and focus-hill type, a large number of burrows and marmots are concentrated in small areas and the maximum daily movement is not more than 100 meters.

Substantially the same is true regarding the southern woodchuck in this country. Observations indicate that animals inhabiting an area sparsely populated with its own kind, travelled much more extensively than those in dense populations.

The home range seems to be directly dependent upon the location of the home den. If the home den is located in a ravine, on a terrace, a woodlot, or odd area, the woodchuck will often travel to pastures, hay fields, and other favorable habitats, sometimes several hundred yards away. If woodchucks locate their dens in a clover field, pasture, or similar favorable habitat, the home range is often restricted to an area within 20 yards of the den, depending on the thickness of the surrounding cover.

Seasonal movements.—Seasonal movements may be divided into three major categories. The first occurs in the spring when the animals emerge from hibernation and move into the field dens. The second occurs as a result of the dispersal of the young from the home den. The third major movement occurs in the fall when the animals move from the summer dens back to the winter areas.

There appears to be a definite rearrangement in the population composition at three times during a year. The first is noticed in the spring when the 'chucks begin their mating activities, again as they move from the winter to summer areas, and in the fall when they move from the summer areas to more favorable winter habitats. One would expect the animals in a field to select the nearest suitable winter area, but such is not always the case. Certain animals will return to a distant hibernation site when there are locations that are apparently just as favorable nearer at hand.

A study of marked animals on the Refuge has conclusively shown that the males are the greatest travelers, associated, at least in part, with the mating activities when the male may sometimes traverse a considerable territory in search of a mate. The female, on the other hand, is less inclined to wander. Two tagged females remained within a few yards of the original trapping location for three and four years respectively.

Observations and trapping records taken during the fall of 1947; spring, summer, and fall of 1948; and spring and summer of 1949 show the following movements in chronological order:

Last recorded date of woodchuck in field den—October 20, 1947
Last woodchuck seen in 1947—November 20
First animal seen in 1948—February 15
First field den occupied in 1948—March 19
Last recorded date of woodchuck in field den—October 22, 1948
Last woodchuck seen in 1948—November 11
First animal seen in 1949—February 14
First field den occupied in 1949—March 23

Quimby (1951) notes woodchucks emerging from hibernation on April 5, 1941 at Cloquet, Minnesota. Smith (1931) gives a calendar of disappearance and emergence for the New England woodchuck, *Marmota monax preblorum*, at Wells River, Vermont. Because of the colder climate the listings show a much earlier disappearance and a later emergence than in Maryland.

The dispersal of the young from the home or natal den occurs in June at the Refuge. One juvenile, tagged for the first time on June 19, 1948, was trapped at another location on June 29, and still another on July 5. Trapping records indicate that there is considerable wandering of some juvenile animals after they leave their home den in late May or June. Very few juvenile woodchucks were trapped at new den locations, indicating that abandoned burrows were utilized for the most part during the first year.

Territoriality.—Hamilton (1934) and Cahalane (1947) both note that the woodchuck exhibits very little territoriality except within the actual confines of the home den.

Animals often feed within short distances of one another without apparent antagonism on the part of any of them. I once observed three large animals feeding within a few feet of each other. When alarmed each took the shortest course to its home den.

Woodchucks will usually guard the home den against all comers, except in the breeding season, when females and males may occupy a single den.

There is some evidence that males exhibit territoriality during the breeding season. An invasion of the territory of a male by other males is likely to result in a fight. On one occasion a larger animal was observed driving a smaller one away, and another observation noted two animals fighting.

ACTIVITY

The woodchuck spends a large part of its life either resting or sleeping in a den. Even during the height of activity in the spring and summer, it spends only an hour or two each day above ground. Depending on the climate, four, five, or even more months are spent hibernating. It is safe to say that the woodchuck spends about 80-90 percent of each year either sleeping or resting.

Many factors, such as time of year, weather, breeding activities, and time of day have either a direct or indirect effect on how each day is spent.

Activity the first week after emergence from hibernation seems to be highly erratic. The weather at this time of year is often changeable, with alternating warm and cool spells. If the weather is warm, considerable activity about the den is evident and the males may begin their wanderings in search of a mate.

Hamilton (1934) advances the theory that in the early part of the year (March in New York, late February and early March in Maryland) wood-

chucks may be as active at night as during the day. His proof seems to be conclusive. Other observers consulted report observations of nocturnal activity. Observations and trapping at the Refuge indicate that while some nocturnal activity was in evidence, most of the movements were diurnal. On March 17-19, 1948, a study of diurnal and nocturnal activities of the woodchuck was made. All known dens were plugged and a trap placed at each location. All burrows were checked at dawn and again at sunset. On the afternoon of the 17th, a woodchuck was found in a trap indicating activity before dark, as the trap had been previously checked in the morning. On the 18th, two cases of diurnal activity were noted. No movement after dark was observed or indicated by opened dens. Again in the first week of March, 1949 nocturnal activity was checked. Two cases of movements after dark were noted as compared with 10 observations during the day, although no warm moonlight nights occurred in the check period. From the studies made at the Refuge, it was concluded that the woodchuck is more active during the day at this time of year, as well as throughout the late spring, summer, and fall.

April 9-10, 1949 were spent in the field in an area of high woodchuck concentrations. Both days were sunny with a mild to strong wind blowing. The nights were cool. Practically all woodchucks seen in the morning were sunning themselves at the den with only a small amount of feeding going on. About 2 p.m. the animals began feeding. All 'chucks shot an hour before sunset had full stomachs. The animals killed earlier in the morning had little, if any, food in their stomachs. Woodchucks were observed in the open continuously from 9 a.m. until almost dark. On a cool, rainy, windy day 48 hours later only a few animals were sighted.

As the spring season diminishes and the days become warmer, the woodchuck goes through a period of transition. The peak of activity gradually changes from the warmest part of the day in the early spring, to morning and evening periods in the summer, and then reverts back to the former peak in the fall.

Whether there is more activity in the evening or the morning in summer is debatable. Trapping records show that activity is about evenly distributed between the periods, but personal observations made while hunting indicate that the groundhog moves around more in the evening. Hamilton (1934) in his New York studies, has arrived at approximately the same conclusion. Although the peak activity is during the morning and evening, woodchucks may be observed at any time of the day, even during the hottest part of the summer.

Biologists at the Rose Lake Wildlife Experiment Station in Michigan (1940-41) observed that woodchucks living in woodlots were not as restricted in their feeding periods as those in open fields. Feeding was noted throughout the day.

Weather plays an important part in daily activity. Usually before a storm, increased activity is observed and is reflected in trapping records. Cool, windy days definitely limit woodchuck movements. If the cool, windy days are accompanied by rain, the animals will remain in their dens throughout the day. On the other hand, a warm light rain will often bring increased activity.

As the fall days become shorter and cooler, the periods of activity of the

woodchuck again change. More and more activity is observed through the warmer, middle part of the day, but it is still not uncommon to see them also in the morning and evening. In late September the larger adult animals begin their long hibernation period. Sometimes a warm day will bring them out for a short time before they disappear for the winter. In October movements are greatly reduced, confined largely to the warmer portions of the day. The same is true of early November when some animals are still active.

SUMMARY

Intensive studies of the woodchuck were carried out on the two farm areas of the Patuxent Research Refuge, Laurel, Maryland, from 1947 to 1949. Extensive studies were made in several localities throughout Maryland. A technique found highly successful in obtaining live animals involved the use of dug-in traps, placed so that woodchucks in the burrow system had no choice but to enter the trap. In handling animals secured in live-traps, a cotton mesh fish bag was found to be more practical than wire cones or burlap sacks.

The species *Marmota monax* is presently divided into nine subspecies, distributed over most of the United States and southern Canada.

The southern woodchuck is distributed through the middle eastern United States, with the largest populations occurring in the Middle Atlantic States. An extension of the range into the eastern shore section of Maryland has occurred within the past 40 years.

The greatest longevity record was ten years. Animals four years of age have been handled at the Rose Lake Wildlife Experiment Station in Michigan and at the Refuge. The natural life span is from five to six years.

Hibernation is progressive, the older and fatter animals going in first, followed by the yearlings and juveniles. The same order of precedence holds true as the animals emerge, the larger ones appearing first. A hibernating captive animal was studied under simulated outdoor natural conditions in 1948-49. Weight loss of a number of animals during hibernation was 30.45 percent and continued for several weeks after emergence.

Length of gestation periods were obtained. Two captive females were mated with a single male, resulting in gestation periods of 32 days (plus or minus one day) and 33 days (plus or minus one day). An artificially inseminated female produced a litter in 31 or 32 days.

An average litter of 4.6 young were recorded from 29 females examined.

Weights proved to be an accurate and practical field method of aging woodchucks. Over 500 weights were obtained during the investigation.

The sex ratio among 215 animals was 1.03 males to 1 female.

The average fall population on the Check Farm was 12 animals per 100 acres, that of the Conservation Farm about 18 per 100 acres. Indications are that the southern woodchuck is increasing throughout most of its range.

Food habits studies in the spring and summer showed that red clover, white clover, grass, chickweed, and alfalfa were the foods eaten most often and in the largest amounts.

Activities of man and predators were the most important mortality factors. Flooding, disease, and parasites were found to be of negligible importance.

Den construction varied according to land use and site. The winter dens located in wooded areas usually had only one entrance, rarely more than two. Summer field dens were characterized by a main entrance, with a mound of fresh soil and a smaller plunge hole, sometimes well concealed in the surrounding vegetation. Excavations conducted during the investigation further substantiated the theory that woodchucks hibernate in plugged off chambers. A total of 22 dens were excavated and only one animal recovered. Woodchucks were widely selective in the choice of soil types but showed a preference for the sandy loams. Well drained and protected situations were the primary factors in selection of winter den sites.

In the winter, the use of woodchuck burrows by rabbits was light when winds were moderate and temperatures above 30° F. Moderate use of holes was noted when the temperature varied between 20 and 30° F. Heavy use was observed when strong winds were blowing and temperatures were below 20° F. Other animals known to frequent dens were skunks, opossums, foxes, raccoons, weasels, wood mice, gray squirrels, jumping mice, chipmunks, meadow voles, shrews, house mice, pine voles, and several species of snakes.

Home ranges were directly dependent upon the location of dens in relation to the habitat. Animals inhabiting dens in ravines, woodlots, and odd areas were often known to travel several hundred yards to feeding areas. Woodchucks in clover and alfalfa fields sometimes restricted their home ranges to an area within 20 yards of the den. Seasonal movements were noted in the spring shortly after emergence from hibernation, in the summer as the young dispersed from the home den, and again in the fall when the animals moved from the summer dens to hibernating areas. Woodchucks exhibited territoriality within the home den.

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* A bibliography containing practically all of the important literature concerning the *Marmota monax* group is contained in the dissertation from which this paper is extracted and is on file at the University of Michigan.

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The Reproductive Cycle of the Mearns Cottontail in Illinois[1]

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Knowledge of breeding habits is usually considered of basic importance in planning for the management of wild game and fur animals. Cottontail rabbits are the leading game species on agricultural land throughout most of the United States, where they are also frequently of considerable economic importance because of their depredations on orchards or field growing crops. In spite of these facts studies of cottontails have very often been passed over in favor of work on more interesting but less important game species. Furthermore, the reproductive cycle of rabbits has been investigated even less adequately than some other phases of cottontail investigation. This paper reports a study made in central Illinois from August 1947, to September 1948, of the reproductive cycle of the Mearns cottontail rabbit, *Sylvilagus floridanus mearnsi* (Allen).

Acknowledgments

Grateful acknowledgments are made to Dr. Donald F. Hoffmeister, Dr. Harlow B. Mills and Dr. Ralph E. Yeatter, under whose guidance and supervision this study was made. Appreciation is also extended to the following: The Illinois Department of Conservation for contributing assistance and information upon request and supplying the necessary permits for out-of-season collecting; Dr. Charles C. Morrill and Miss Emily Dorstwitz of the College of Veterinary Medicine and Hygiene, University of Illinois, for their assistance in the preparation and interpretation of histological material; Mr. Charles Scott for his assistance in photography; Mr. Robert Ellis and Mr. Walter Hart for their help in collecting rabbits; and to Mr. James Ayers for his editorial contributions. The microphotography was done by a professional photographer with the assistance of the writer.

Methods

Gonads were removed from the rabbits as soon as possible after collecting. After being weighed and measured, the gonads were fixed for 24 hours in Zenker's solution. Thereafter, they were imbedded in paraffin and sectioned on a rotary microtome. The paraffin sections were placed on slides and washed free of traces of fixative, then stained with iron hematoxylin and mounted in clarite.

Courtship and Mating

The courtship of cottontail rabbits as observed during the present study was found to be a highly animated and somewhat elaborate performance. Apparently the pre-mating and mating behavior of these rabbits have not previously been described in detail. Dalke (1942) described the courtship in part as observed among penned cottontails. He also reported an observation on wild cottontail rabbits in which, apparently, four males were trailing a female in heat. Trippensee (1934) and Brown (1935) reported briefly on the mating behavior of cottontails.

1 Extraction from a thesis submitted to the University of Illinois as partial fulfillment of the requirements for the degree of Master of Science.

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On the morning of April 22, 1948, during field studies near Urbana, Illinois, Dr. Donald F. Hoffmeister and the writer observed under exceptionally favorable conditions the entire series of events in the courtship and mating of a pair of Mearns cottontail rabbits. Observations were made from a car parked near a 10-acre bluegrass pasture in which three cottontails were first observed at 6 A.M. The pasture was almost level and the grass was not over five inches tall, permitting good visibility with the aid of field glasses of all parts of the field.

Of the three rabbits under observation, two were leisurely hopping from one clump of grass to another, occasionally eating a few blades of grass. Subsequent events indicated that these latter rabbits were non-receptive females. The third, which proved to be a male, was obviously in a high state of excitement and was constantly on the move. His fur was quite wet from his repeated forays through the dew-covered grass.

From 6 A.M. to 6:25 A.M. this male cottontail moved in a series of runs twice around the margin of the field and, in addition, he made several crossings through the center. He may have recognized the scent of the other rabbits when he crossed their trails, for once he appeared to follow a trail as he ran up to one of the rabbits, and jumped over it, but he showed no further interest in it. Later, he moved to within 4 feet of our car and sat on his haunches while inspecting us thoroughly. Apparently having satisfied his curiosity, he hopped away without displaying the slightest alarm.

At 6:25, it was suddenly apparent that he had found a trail which greatly interested him. He followed the trail rapidly with his nose close to the ground until he found a fourth rabbit. This rabbit, obviously a receptive female, up to then had escaped the attention of the observers. The subsequent courtship and mating behavior was observed at close range. The pattern of the courtship performance can be summarized in a few words. The male, always the aggressor, would approach the female until they faced each other at close range. After remaining motionless for a few minutes, the male would advance and the female would then issue a rapid series of blows at him with her front feet. Immediately, and seemingly as part of the same swift action, one or the other of the rabbits would jump upward about two feet while the other would dash under the arc of the jump. As it jumped, the rabbit would twist in the air so as to alight nearly facing the other animal. The whole action, from the approach of the male to the completion of the jump, took place with split second timing. It was repeated over and over, with first the male and then the female making the jump while the other scurried underneath. As mentioned, however, the male always initiated the action by advancing toward the female.

This sparring game continued for about 15 minutes before the female allowed the male to attempt copulation. She turned from him once but the second time allowed him to mount. In mounting the male grasped the female about the flanks with his front feet and held his head high. As he did so, his hindquarters were brought forward, but no further thrusting was observed. Contact lasted only two or three seconds, after which the male backed off.

After copulation the female hopped unhurriedly away with the male close behind. Two or three more feints and jumps were made by the pair but with much less vigor than before. In a few minutes the two parted company. The

male, whose sexual excitement was evidently spent, now behaved normally, eating a little grass and making one or two leisurely runs.

MALE BREEDING CYCLE

Several writers have relied on increased testicular weights combined with general appearance of testes (in scrotum or not in scrotum) as an index to male sexual activity in rabbits. Trippensee (1936) and Schwartz (1942) both agreed that the above criterion is usually reliable, but that the rule is occasionally unreliable. Dalke (1942) made paraffin sections of testicular material, but many of his sections were incomplete and others were poorly prepared. Because of the inaccuracy involved when using the appearance or weight of testis to judge breeding condition, the system was not adopted for this study. Instead, the more accurate method of micro-examination of testis sections was employed. The season of male sexual activity was, therefore, determined by preparing a complete monthly series of testis sections and thus noting the varying degrees of spermatogenesis, the amount of maturation, and particularly the amount of sperm found in the epididymis.

Testicular material from 30 rabbits was thus collected and prepared between November 1947 and September 1948. From this series of slides the male breeding cycle was determined for 1948. Early in the study it was discovered that the rate of maturation varied considerably in different seminiferous tubules within the same testes. The best criterion of breeding condition was, therefore, found to be the amount of sperm present in the epididymis.

Table 1 summarizes the evidence of the male reproductive cycle as determined from the study of slides. Although apparently mature sperm began to appear in the seminiferous tubules of rabbits as early as mid-January, there was no heavy accumulation of spermatozoa in the epididymides until late in February. Since it is necessary that an adequate supply of spermatozoa be stored in the epididymis before fertile coitus can be accomplished (Hamlett, 1938) it is doubtful that many male cottontails were capable of breeding in central Illinois much before the middle of February in 1948. At least, as will be shown under the section on "Female Breeding Cycle," no record of fertile breeding was recorded earlier than the last week of February 1948. Spermatozoa appeared in sizable numbers in the epididymides of male rabbits from one to three weeks prior to any record of fertile coitus. It is then assumed that the starting date of reproduction in the cottontail is largely dependent on the physiological or psychological condition of female rabbits because males appear to reach sexual readiness somewhat earlier than females.

The data in table 1 indicate that male rabbits maintained a high sexual activity through July and well into the month of August. A noticeable decline in testicular activity did not occur until late August and absolute cessation of maturation divisions did not take place until sometime later (exact date undetermined). From table 1 it will also be noted that in early spring sub-adult male rabbits (under 9 months of age) came into breeding condition later than adults (see data on rabbits 46 and 55, table 1). The weight of the testes of young males was also considerably less in these cases. By the time the breeding season was well under way (April 1) the sub-adult rabbits were producing sperm fully as fast as the older animals.

Photomicrographs were taken of testes in all stages of spermatogenesis

TABLE 1.—Summary of cottontail testes study

Rabbit No.	Age	Date Collected	Presence of Sperm Cells in Seminiferous Tubules	Presence of Sperm Cells in Epididymis Tubules	Testis Weights (grams)
15	Adult	11/16/47	0	?	(undescended)
....	Adult	1/17/48	1	?	?
....	Adult	1/25/48	3	?	?
42	Adult	2/12/48	3	1	(descended)
47	Adult	2/15/48	3	2	(descended)
48	Adult	2/15/48	2	1	(descended)
58	Adult	2/22/48	4	4	23.7
60	Adult	3/28/48	3	3	28.4
61	Adult	4/ 1/48	4	4	25.0
70	Adult	5 /2/48	4	4	27.0
71	Adult	5/ 2/48	4	4	28.5
72	Adult	5/ 5/48	4	4	27.7
74	Adult	5/ 5/48	4	4	33.0
81	Adult	6/10/48	4	4	22.0
82	Adult	6/15/48	4	4	25.0
84	Adult	6/17/48	4	4	21.5
85	Adult	6/17/48	4	4	21.5
87	Adult	6/25/48	4	4	23.7
88	Adult	7/ 3/48	4	4	21.0
91	Adult	7/12/48	4	3	20.0
92	Adult	7/30/48	4	4	22.0
93	Adult	8/ 4/48	3	4	17.5
4	Young	9/13/47	0	0	?
46	Young	2/15/48	2	?	?
55	Young	2/15/48	1	?	11.3
66	Young	4/ 1/48	4	4	26.0
78	Young	5/ 5/48	4	4	18.0

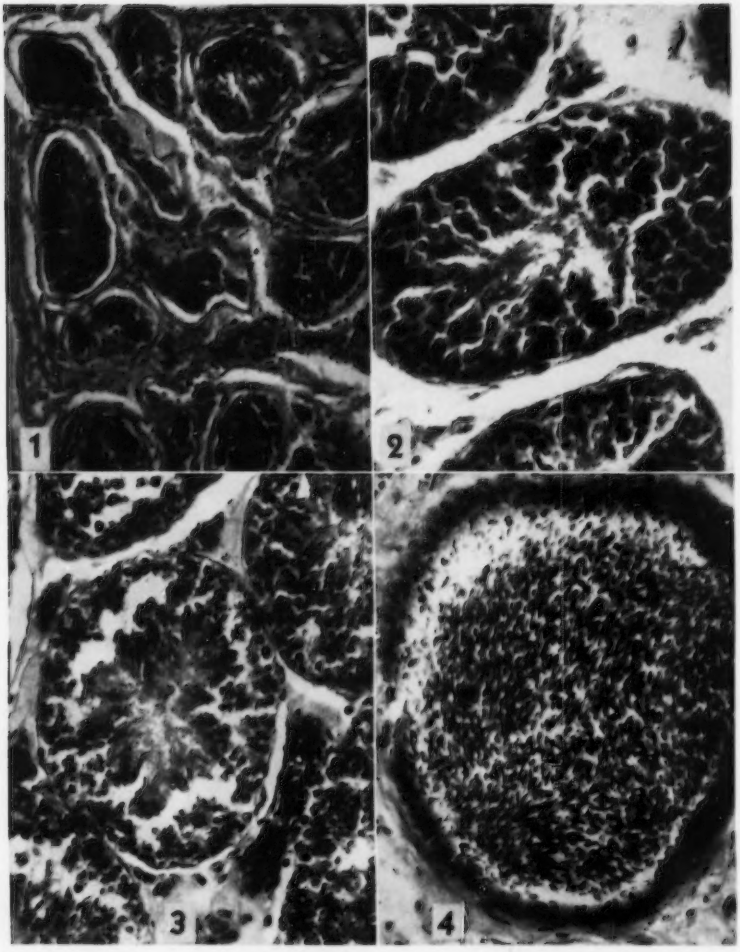
Key to table 1: *Column* 2—adult age—over 9 months. *Columns* 4 and 5—1. very few mature sperm cells present, 2. moderate number of mature sperm cells present, 3. sperm cells rather numerous, 4. sperm cells extremely numerous.

from November through June of 1948, exclusive of December and March. Figures 1 through 4 show various stages of male gonads during the 1948 breeding season. The different stages were recognized with the aid of an account of rabbit spermatogenesis as described by Marshall (1922).

Within the limits of the active male breeding season (from February 15 to August 10) there was a range in testes weights between 20.0 grams and 33.0 grams (table 1). This wide range in testicular weights could not be attributed to different rates of function because all gonads were found to be functioning to near capacity, and a comparison of body weights with testis weights showed only a rough correlation. It is therefore, evident that the only reliable means of determining male reproductive capacity from the collected specimens is through micro-examination of the gonads.

FEMALE REPRODUCTIVE PROCESSES

Studies by Marshall (1922), Hammond and Marshall (1925) and Allen, Danforth and Doisy (1939) have contributed quite thoroughly towards the



Figs. 1-4. Cross sections of adult rabbit testes.—1. Collected Nov. 16, 1947; spermatogonia and spermatocytes present but no evidence of maturation; 2. Collected Jan. 17, 1948; all stages of spermatogenesis present; only a few mature spermatozoa present; 3. Collected Feb. 12, 1948; seminiferous tubules showing rapid rate of spermatogenesis; 4. Collected Feb. 22, 1948; epididymis solidly packed with mature sperm cells.

knowledge of reproductive processes in domestic rabbits. Even though the cottontail belongs to a different genus the processes of female reproduction closely parallel those known for its domestic relative except for one or two minor exceptions. In describing these processes the writer has drawn rather liberally from the above three citations.

During the winter months, rabbits generally are in a quiescent or anoestrous period, at which time follicular growth in the ovaries is greatly suppressed.

While rabbits are in anoestrous, their follicles develop to a certain extent, but the maturation of follicles does not occur. Towards the end of the anoestrous period some external stimulus (as yet undetermined) causes the pituitary gland to secrete a follicle stimulating hormone (F. S. H.) which is transferred by the blood to the ovaries. This hormone acts as a somatic nutritive and stimulates growth of the follicles and development of the ova. The ova thus develop to a submature stage during which time the rabbit is said to be in heat and remains in heat until coitus occurs. The nervous stimulation of mating causes the pituitary to secrete another hormone, luteinizing hormone (L. H.), which causes the eruptive growth of the follicles and the process of ovulation. Ovulation occurs about 10 hours after coitus and subsequently the ova are fertilized in the fallopian tube. The fertilized ova enter the uterus on about the fourth day and become implanted on the seventh day, at which time the blastocyst is at the 1 to 5 millimeter stage.

If coitus does not occur, the female rabbit may remain in heat for long periods. While the rabbit is in heat, submature follicles are present in the ovaries at all times, and the old follicles either remain or are replaced by newly developed ones.

No true oestrus cycle is experienced in rabbits since ovulation does not occur unless stimulated by an orgasm. However, an orgasm is occasionally experienced without fertilization having taken place (either by the act of one doe attempting to copulate with another or by coitus with an infertile buck) after which a state of pseudopregnancy develops. Pseudopregnancy in rabbits is the only physiological process which resembles the oestrus cycle of most other mammals. During pseudopregnancy, corpora lutea are formed in the ovaries and follicular growth is retarded.

Soon after ovulation occurs, corpora lutea form at the sites of the follicular ruptures and remain throughout the duration of pregnancy. As long as the corpora lutea remain active they secrete progesterone, which in turn prevents the formation and ovulation of other mature ova. Towards the end of pregnancy the corpora lutea usually start to decrease in size. Then the placenta takes over the secretion of progesterone. Within a few hours after parturition and the consequent stop of progesterone secretion, mature follicles again appear in the ovaries. It is, therefore, common for rabbits to have fertile coitus very soon after parturition.

The somatic nutriment which supplies stimulation to follicular and embryonic development is also involved in the stimulation of the mammary glands for the secretion of milk. Many domestic rabbits which become pregnant soon after giving birth to large litters (5 or more young) are unable to supply enough nutriment for both the suckling litter and the embryonic litter. As a result, resorption of the embryonic litter often results between the 8th and 15th day of development. However, total resorption of an embryonic litter appears rare among cottontails, perhaps because the wild rabbit often has smaller litters and also because it suckles its young for a much shorter time than does the domestic species.

FEMALE COTTONTAIL REPRODUCTIVE CYCLE

The exact breeding season for cottontails is apparently controlled by the females, although the external factor or factors which stimulate female sexual

TABLE 2.—Breeding data for 6 rabbits collected on April 1

Rabbit No.	Lactating	Pregnant	Aver. Size of Embryos (mm)	Age of Embryos[1] (days)	Days Since First Breeding[2]	Approx. Date of First Breeding
62	yes	yes	1	5	35	Feb. 24
63	yes	yes	1	5	35	Feb. 24
64	no	yes	18	16	16	Mar. 15
65	no	yes	18	16	16	Mar. 15
67	no	no[3]			15	Mar. 16
68	no	yes	9	12	12	Mar. 19

[1] After Schwartz (1942). [2] Allow 30 days for full term of lactating litters plus age of embryonic litters. [3] Pseudopregnancy of about 15 days duration as described by Hammond (1922).

development are likely the same factors which control the onset of spermatogenesis in the males. It was seen above that most males were sexually active by February 15, 1948. No pregnant females (or females which had recently ovulated) were found prior to February 22. It is, of course, assumed that since nearly all mature males were capable of breeding by this date, that a female arriving in heat would have received quick service.

The average gestation period in cottontails is about 30 days, with the range being between 25 and 32 days (Seton, 1929; Dice, 1929; Prouty, 1937; Gerstell, 1937; Dalke, 1942; and Haugen, 1942). Aging technique for embryos has been developed by Schwartz (1942) for the cottontail in Missouri. By using this knowledge the first breeding date for six cottontails collected on April 1 (rabbits 62 through 68—table 2) was estimated to have taken place between February 24 and March 20. It is assumed in the cases of rabbits 62 and 63 which were pregnant and lactating that the second litters were conceived very shortly after parturition of the first.

Another check on the initial date of the breeding season was the evidence collected from early nests. The approximate age of nestling rabbits can be determined by knowing the approximate size at birth, the approximate age when eyes and ears open, and knowing the approximate age when leaving the nest. This information is submitted under another title later in the manuscript. The nestlings in these cases were observed long enough to determine within one week the exact date of birth. By noting the approximate age of nestlings and subtracting their age, together with the 30-day gestation period, from the date on which the nest was found, the approximate date of conception was estimated. Six occupied nests were found between March 29 and May 2 of 1948. Of those six litters, two were conceived during the last week in February and four were conceived between the 17th and 21st of March (See table 3).

From the above cases of early pregnancies and early nests it is evident that the breeding season of 1948 got under way during the last week in February 1948, and that all the females did not arrive at oestrus (desire for coitus) on the same date. The first two weeks in March probably mark the time when the majority of breeding got under way although some activity had commenced a week or so earlier.

TABLE 3.—Reproductive data on cottontails for central Illinois

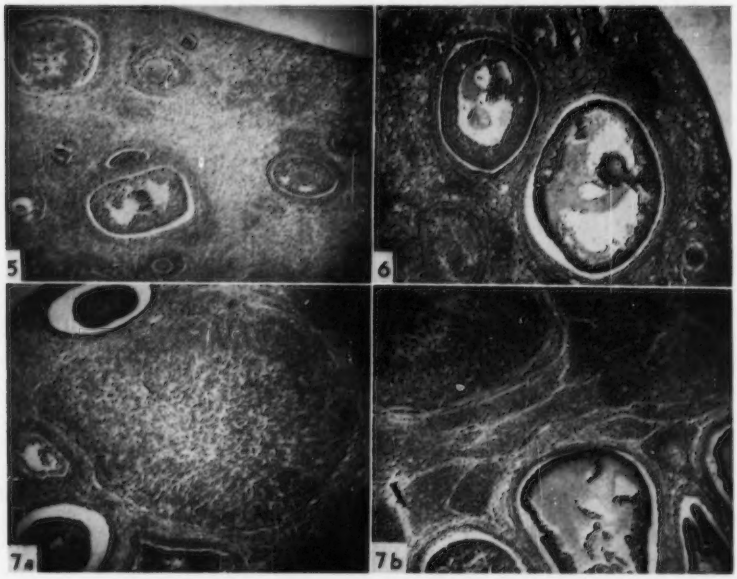
Rabbit No.	Date	Age	Con. of Uterus	No. of Young	Lactating	No. of Plac. Scars	C.L. or C.A Size (mm)	Size of Graaf. Foll. (mm)
36	7/ 3/47	Ad.	R.P.	....	?	6	CA—1.2	.40
5	9/13/47	Yg.	Im.	....	....	0	No	.44
6	9/13/47	Yg.	Im.	....	....	0	....	....
9	9/23/47	Yg.	Im.	....	....	0	....	....
11	10/ 1/47	Yg.	Im.	....	....	0	....	....
12	10/ 1/47	Ad.	Sh.	No	No	3	....	....
16	11/16/47	Ad.	Sh.	No	No	5	No	.56
18	11/16/47	Yg.	Im.	....	....	....	....	....
30	11/30/47	Ad.	Sh.	No	No	?	....	....
31	11/30/47	Yg.	Im.	....	....	....	....	....
33	11/30/47	Ad.	Sh.	No	No	?	No	.40
35	12/19/47	Ad.	Sh.	No	No	?	No	.3
38	1/ 4/48	Ad.	En.	No	No	?	No	.72
43	2/13/48	Yg.	?	No	No	0	No	.52
45	2/13/48	Ad.	?	No	No	0	No	.72
51	2/13/48	Ad.	?	No	No	0	No	.80
52	2/15/48	Ad.	Vas.	No	No	0	No	.80
53	2/15/48	Ad.	?	No	No	0	No	.64
56	2/15/48	Ad.	?	No	No	0	No	.80
57	2/22/48	Ad.	Vas.	No	No	0	No	.80
62	4/ 1/48	Ad.	E.P.	7	Yes	....	CL—1.6-1.7	.5
63	4/ 1/48	Ad.	R.P.	?	Yes	4	CL—just form	1.0
64	4/ 1/48	Ad.	E.P.	7	No	....	CL—1.92	1.0
65	4/ 1/48	Ad.	M.P.	6	No	....	CL—1.4	.50
67	4/ 1/48	Ad.	P.P.(L.)	?	No	....	CL—1.2	.30
68	4/ 1/48	Ad.	M.P.	7	No	....	CL—1.6	.50
73	5/ 5/48	Ad.	L.P.	7	Yes	....	CL—1.4	.40
75	5/ 5/48	Ad.	L.P.	9	Yes	....	CL—1.7	.30
76	5/ 5/48	Ad.	L.P.	7	No	....	CL—1.6	.50
77	5/ 5/48	Ad.	L.P.	8	Yes	....	CL—2.2	.50
83	6/15/48	Ad.	L.P.	6	Yes	....	CL—1.4	.50
85b	6/21/48	Ad.	R.P.	No	No	5	?	.50
86	6/25/48	Ad.	M.P.	3	Yes	....	CL—1.4	.50
90	7/ 6/48	Yg.	?	....	No	....	CL— .8	.50
94	8/ 5/48	Ad.	L.P.	5	Yes	....	CA	....
95	8/ 6/48	Ad.	E.P.	6	Yes	....	CL	....
96	8/11/48	Yg.	E.P.	7	No	....	CL	....
Averages				6.5		4.7		

Key to table 3: *Column* 3: Ad.—Adult, Yg.—Young. *Column* 4: R.P.—recent pregnancy, Im.—immature, Sh.—Shriveled or shrunken, En—Enlarged, but not vasculated, E.P.—Early pregnancy (1 to 10 days), M.P.—Median pregnancy (11 to 21 days), L.P.—Late pregnancy (over 21 days), P.P.—Pseudopregnancy. *Column* 7: Plac.—Placental. *Column* 8: C.L.—corpus luteum, C.A.—corpus albicans. *Column* 9: Graaf. Foll.—Graafian follicle.

While autopsying rabbits the condition of reproduction for all females was noted. In some cases it was found that a macro-examination was insufficient to diagnose the stages of reproduction. In order that more accurate interpretation could be made, paraffin micro-sections were prepared from many of the ovaries collected between July 3, 1947 and August 6, 1948. Table 3 sum-

marizes the results of the female reproductive study for this period. Photomicrographs were made of 16 ovaries in different physiological stages of reproduction. Figures 5 through 8 show the various stages encountered.

In interpreting these cross sections, it is not necessary to recognize the early stages of oogenesis because the process is going on at all seasons even in immature animals. Primordial ova are present in the ovaries of all normal animals. The important things that will be pointed out are (1) the growth and maturation of ovarian follicles, (2) active corpora lutea, (3) corpora albicans, and (4) follicular degeneration or atrophy.



Figs. 5-7b. Female reproductive stages.—5. Collected Nov. 16, 1947; follicular growth is retarded in the non-breeding season; 6. Collected Jan. 4, 1948; some follicular growth increase but atrophy commences prior to maturation; 7a. Collected April 1, 1948; rabbit was suckling one litter and was pregnant with the second litter; 7b. Collected April 1, 1948; advanced stage of pseudopregnancy.

A description of the process of follicular atrophy is submitted. This description has been taken directly from Marshall (1922:150-151):

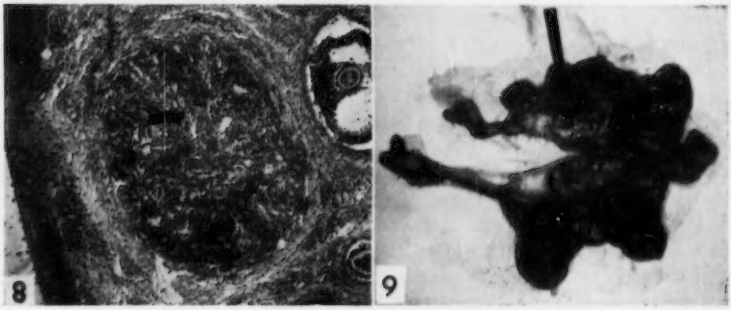
"The following characteristics serve to distinguish the degenerate or atretic follicle . . . from the true corpus luteum: (1) There is no indication of any rupture to the exterior. (2) The ovum, being retained in the follicle, loses its regularly circular shape, becomes shrivelled, and gradually disappears altogether. (3) The follicular epithelium, instead of hypertrophying, degenerates the chromatic substance at one stage often appearing in the form of fine points in the cytoplasm, and much smaller than nuclei. Subsequently, the remains of the cells become unrecognizable, finally disappearing altogether. (4) The connective tissue wall does not proliferate to form a network among the epi-

thelial cells, and there is generally no ingrowth from the thecae until the epithelial cells are in an advanced state of degeneration or have altogether disappeared. The earliest indication of atretic change is usually seen in the chromatolytic changes in the epithelium. Afterwards the theca interna degenerates, and then the ovum and zona pellucida."

RESORPTION IN COTTONTAILS

Hammond and Marshall (1925), working with the domestic rabbit, reported that the suckling of four or more young by a female results in the total resorption of a new embryonic litter usually between the 8th and 15th days. Lactation in cottontails apparently does not result in the resorption of embryos. Schwartz (1942) recorded two cases of possible total resorption and three of partial (only part of the litter) resorption. In the cases of total resorption, Schwartz reported, "It is possible that embryos were present though too small to be seen." Only one of these cases could possibly have been due to excessive lactation since the other four animals were not lactating. This fifth case (in August) was one of the doubtfuls.

The one case of resorption discovered in the present study was found on June 25, 1948. In this case the female was heavily lactating, but only one of four embryos had been resorbed (See fig. 9). In cases of resorption due to excess lactating in domestic rabbits the entire embryonic litter is usually resorbed. Since three of the embryos were normal in this case, it does not seem probable that death of the fourth was caused by somatic starvation due to excess lactation.



Figs. 8-9.—8. Juvenile, collected July 6, 1948; ovary shows signs of recent ovulation; 9. Partial resorption (one of litter); not common in cottontails

Between April 1 and August 6, 1948, thirteen pregnant females were collected. Three of the rabbits, all collected on April 1, were probably in the advanced stages of their first pregnancies, but of the remaining ten rabbits nine were heavily lactating while carrying a later litter *in utero*. Five of the nine were in an advanced stage of pregnancy, 20 days and over, and three were in an earlier stage. No resorption was evident in any of the nine. Of course, it is impossible to tell how large a litter any of these rabbits was suckling but judging from the data on average litter size, it is quite probable that at least some of these nine rabbits were suckling five or more young. It then seems

safe to conclude that cottontails are normally capable of suckling one litter without depriving somatic nourishment to embryos in utero.

LACTATION

The lactation period for domestic rabbits is usually from 35 to 40 days. It has been generally conceded that the lactation period for cottontails is much less. Allen (1938) surmised a 16-day lactation period for one litter of *S. f. mearnsi*, basing his conclusions on the length of time the young remained in the nest. Dalke (1942), with captive cottontails, found the period to range between 14 and 16 days for two subspecies of eastern rabbits (*Sylvilagus floridanus mallurus* and *S. transitionalis*). He also determined the length of the period by the amount of time the young were in the nest. The present study indicates that the lactation period may be longer than 16 days.

As previously mentioned, five lactating females were autopsied which were at least 20 days pregnant, the embryos all measuring over 39 mm. One of these five, No. 83, had embryos that measured between 90 and 100 millimeters in length and was presumed to be about ready for parturition. Assuming that a new pregnancy immediately followed the parturition of the previous litter, and that lactating females can be determined as such by the presence of milk together with the absence of nipple plugs, lactation in these five cases lasted for at least 20 days; and in the case of the 90-100 mm embryos, about 30. It is probable that lactation declines sharply between the 14th to the 16th day when the young disperse from the nest and start eating greens, but the above evidence indicates that it may not stop altogether.

Observations on a litter of cottontails under natural (wild) conditions showed that at least two young remained in the immediate vicinity of their old nest for at least a month from the time the nest was abandoned. It is not known if they nursed during this time, but it would have been possible for the mother to find them if she had so desired.

A litter of six rabbits, raised by the writer's wife, drank condensed cow's milk daily for six weeks after which time no more milk was offered. The taste or desire for this milk did not subside as the diet was supplemented with solid foods.

It is, therefore, indicated that young cottontails are nursed to some extent for at least four or five days after leaving the nest, and perhaps, in some cases, until the next litter is born. The lactation period for some cottontails in Illinois may be from 20 to 25 or more days.

FACTORS CONTROLLING RABBIT REPRODUCTION

There has been considerable speculation as to what external stimulus is responsible for controlling the length of the breeding season in cottontails. The direct stimulus from pituitary secretions, is, of course, responsible for the increased activity of gonads at the onset of the breeding season, and the decreased supply of hormones causes the retardation of gonad activity at the close of the season. No one, however, has adequately demonstrated what external factor or factors are responsible for the changes in pituitary action.

Hammond and Marshall (1925) suggest that two conditions may be responsible for setting the limits of the breeding season of domestic rabbits. These are diet and temperature. Rabbits that were kept on a diet of succulent

food throughout the year maintained breeding capacity during the whole time. On the other hand, rabbits fed on an inadequate diet tended to breed in the regular breeding season.

Bissonnette and Csech (1939) were able to promote testicular growth and the appearance of testes in the scrotum by subjecting rabbits to increased daylight in the mid-winter. Sperm formation was accomplished in 23 days in December and January. (The present study revealed natural sperm formation —spermatogenesis—on January 17.) Breeding with females (also subjected to increased light) was accomplished, but no young were produced before April. The change in photoperiod as an important reproductive factor is little more than indicated by this evidence.

There does seem to be a rather close correlation between the limits of the breeding seasons and the availability of succulent vegetation. Throughout the east and midwest, breeding is rather closely correlated with the growing season, mainly March through August. In central California, Orr (1940), working with the Audubon cottontail (*S. auduboni*) found the breeding season for this species to last from December through June. The time corresponds to the wet season when succulent growth is naturally available. Ingles (1941), working with the same species in the Sacramento Valley of California, found that the breeding season there lasted throughout the year. This is significant in that the irrigation practices which are carried on in that part of California may provide succulent growth throughout the year.

The foregoing facts suggest that some component of green vegetation, possibly Vitamin E, is responsible for stimulating the pituitary glands of rabbits into the secretion of somatic nutritives, and consequently, determining the breeding conditions of the animals.

If this is true we may inquire why spermatogenesis of Illinois cottontails begins in mid-January when no green vegetation is available. A possible explanation for this is that male rabbits can procure enough nutriment from early developing seeds and buds to excite the pituitary. We do know that considerably less stimulus is required to bring male gonads to maturity than is needed for ovarian development (Allen, Danforth and Doisy, 1939). It is recalled from a foregoing discussion that while spermatogenesis commenced in mid-January, actual breeding did not get underway until late in February, at which time some green vegetation was available.

RAISING OF YOUNG

Nesting.—Thirteen nests were found during the study, most of which were in city areas such as lawns, gardens, and flower beds. Two of the nests were in bare soil with no vegetative cover in the immediate vicinity; the others were in grass or short herbaceous vegetation.

In building the nest, the female digs a cup-like excavation about four inches deep, four to five inches wide, and six inches long. This depression is first lined with leaves and then, on the inside, with hair plucked by the female from her body. Hamilton (1940:10) states, "The removal of the hair from the belly of the rabbit for nest lining serves a dual purpose. Not only does it provide a warm container for the reception of the young, but it provides easier access to the very small nipples." A cover of hair and grass provides concealment and warmth for the young during the mother's absence from the nest.

Litter size.—Litter sizes were estimated from numbers of placental scars, numbers of embryos, and numbers of nestling young. The average litter size indicated by 5 placental counts was 4.7; the average of 13 embryo counts was 6.5; and the average number of young in 13 nests was 4.9. The wide variation was probably due to a seasonal difference in collecting. Most sets of embryos were collected at the season of maximum reproduction (April through June). By combining all three sources, we get from a total of 31 litters, an average of 5.6 young per litter (tables 3 and 4). The approximate dates of birth were computed by judging the ages of embryos, noting the ages of litters, and estimating some dates of birth from placental scars. The estimate of date of birth may be incorrect from one to five days. It is noted that early litters, born in March and early April, are small (4 or 5) and litters born in late April and May are larger (6 to 9). After the first week in June the numbers per litter again fall off to a smaller average.

Feeding periods.—Trippensee (1936) states that the mother cottontail nurses the young by crouching over the nest.

Buele's (1940) observations on Mearns cottontails in Pennsylvania led him to believe the young are nursed only twice in 24 hours, once at dawn and once at dusk.

Limited data collected during this study lends support to Buele's observations and suggests that only one nursing period may be required in 24 hours.

Through the use of an electro-mechanical recording device modified after Kendeigh (1930) records were made at two different nest sites of the frequency of adult visitation to the young, presumably for the purpose of nursing. Successful records were made for only three 24-hour periods (two at one nest and one at the other) but in all three cases only one visit to the nest was made during the 24 hours. All three visits took place in early evening, from 7:30 to 9:20 P.M. In one instance the adult remained on the nest for 45 minutes.

A two-week-old cottontail which had been frightened from its nest in early morning on May 24, 1948, was taken dead from a dog at about 11 A.M. of the same day. This young rabbit weighed 50 grams. Its stomach was filled with curdled milk and a trace of green vegetation. The stomach contents weighed 8.4 grams, or about one-sixth of the rabbit's total weight. Even though the young rabbit may have suckled after leaving the nest, the capacity for so much food in the digestive tract gives further support to the belief that only one or two nursing periods in 24 hours are required by nestling cottontails.

Growth and behavior of young.—Cottontails are covered with fine hair at birth. Since the short hairs are closely pressed against the skin, the young cottontail has the appearance of being naked. The eyes of new-born rabbits are tightly closed and the ears are closely pressed to their heads. The legs are well enough developed to enable them to crawl into the depths of their nest. The new-born cottontail weighs between 35 and 45 grams, is from 90 to 110 mm long, and has an average hind foot length of from 21 to 23 mm, judging from the following data.

Six embryos, nearly full term, collected on June 15, 1948, measured between 90 and 98 mm in length; had hind foot lengths between 19 and 20 mm; and weighed between 30.3 and 38.0 grams each. A nestling litter of 6 (measurements on three) which was known to be four days old on April 20, weighed

between 37 and 43 grams each and had an average hind foot length of 26.5 mm. Another litter of three, which was estimated as three or four days old on March 29, weighed between 43 and 57 grams each, were 100 to 115 mm long, and had lengths of hind foot of 26 mm, 26 mm, and 27 mm, respectively.

Three litters of nestling cottontails were hand-raised on canned milk and water (50:50) during this study. Although these nestlings did not get the same diet that wild rabbits might, it is believed that development closely paralleled that of wild cottontails. The young were able to crawl actively about very soon after birth. At three or four days they could "squeal" and they would thoroughly lick themselves after eating. Their ears occasionally pricked up on the fourth and fifth days. Between the fifth and eighth days, the eyes opened. In some young the eyes opened on the fifth day; in others not until the eighth. The hair was no longer appressed to the body on the 10th day, but was fluffed up. Greens were nibbled on the 12th and 13th days. Somewhere between the 14th to the 16th days the young rabbits started to hop actively about and leave the "nest." During the time of nesting age they gained about two to five grams daily, and the hind foot increased about one millimeter per day.

Aging young rabbits.—Weight is not an accurate criterion of age in young rabbits because of the wide variation among individuals. The weights of littermates often vary as much as 15 or 20 percent of the mean even before the nest is abandoned. The heaviest rabbit in one nestling litter was 57 grams, while the lightest was 43 grams, which is a difference in weight of 14 grams or about 25 percent of the heavier weight. In another litter the variation was from 37 to 43 grams, or a difference of 17 percent. In still another litter the variation was from 55 to 66 grams, or a difference of 15 percent. With such variations between members of the same litter, one can appreciate the variations that might exist between even-aged animals of unrelated litters. Even when littermates start out with essentially the same weights, growth is often not parallel.

A litter of five was raised in captivity from the time they were about 10 days of age. These were kept together and given the same opportunities for securing food and water and were fed identical diets. The conditions in captivity were probably more uniform than those to which rabbits are subjected in the wild. Almost daily weights were kept on the rabbits until they were about 45 days old. They were weighed at about the same time every day. The two extremes in this litter weighed 66 and 60 grams, respectively, or within 10 percent of each other at the start of the experiment. At 45 days of age (36th day of the experiment) the two weighed 340 and 250 grams, respectively, which is a 26 percent difference in their weights. The remainder of the litter fell between these two extremes.

Measurements were also kept of the ears and total lengths for a few days, but a wide variation was encountered at an early date. Measurements of these parts were thereafter discontinued.

Length of hind foot is by far the most standard measurement for cottontails of a given age. Variations within a nestling litter are seldom more than 2 mm, but even the length of hind foot becomes increasingly unreliable as the rabbits grow. The length of hind feet of two litter-mates were recorded from 10 days to 45 days of age. At the start, the hind foot of each measured 37 mm, but after 36 days of growth the two measured 60 mm and 67 mm,

respectively, which is a difference of 10 percent. Even the hind foot measurements are thus too variable to be used as an accurate age indicator for young rabbits. We must thereby conclude that no method could be found to accurately age living cottontails beyond the nestling age (16 days).

Sociability of young cottontails.—When confined together young cottontails get along harmoniously for about seven weeks. At seven weeks of age intolerance begins to appear and the rabbits begin to inflict wounds on each other. A litter of three rabbits was kept together in a small pen until they were about 8 weeks old. On a night during the eighth week one of the young killed a second and badly injured a third litter-mate. This intolerance may be a natural trait which serves as a dispersal factor for young cottontails.

Rate of reproduction.—The breeding season for cottontails in central Illinois extends from the last week in February into the month of September. It is mathematically possible that cottontails, with a 30-day gestation period and a tendency to breed soon after parturition, could produce six or seven litters per season. However, the data collected during this study indicate that fewer litters are actually produced.

TABLE 4.—Cottontail litters

Date Found	Source	Date of Birth (approx.)	Departure from Nest	Date Fertilized (approx.)	Size of Litter
6/10/47	Nest	6/ 4/47	....	5/ 4/47	4
7/ 3/47	Pla. Scar	....	....	....	6
10/ 1/47	Pla. Scar	....	....	....	3
11/16/47	Pla. Scar	....	....	....	5
3/29/48	Nest	3/25/48	....	2/23/48	4
4/ 7/48	Nest	3/27/48	4/10/48	2/25/48	4
4/ 1/48	Pla. Scar	3/28/48	....	....	4
4/20/48	Nest	4/15/48	....	3/16/48	4
4/ 1/48	Embryonic	4/15/48	....	3/16/48	6
4/ 1/48	Embryonic	4/15/48	....	3/16/48	7
4/16/48	Nest	4/16/48	....	3/17/48	7
5/ 2/48	Nest	4/18/48	....	3/19/48	6
4/ 1/48	Embryonic	4/20/48	....	3/21/48	7
4/26/48	Nest	4/20/48	5/ 5/48	3/21/48	7
4/ 1/48	Embryonic	4/25/48	....	3/27/48	7
5/17/48	Nest	....	....	....	6
5/ 5/48	Embryonic	5/13/48	....	4/13/48	7
5/14-20/48	Nest	....	....	....	4
5/ 5/48	Embryonic	5/14/48	....	4/14/48	7
5/26/48	Nest	5/14/48	5/30/48	4/14/48	5
5/ 5/48	Embryonic	5/15/48	....	4/15/48	9
5/ 5/48	Embryonic	5/15/48	....	4/15/48	8
5/17/48	Nest	5/15/48	....	4/15/48	6
6/17/48	Nest	6/ 2/48	6/18/48	5/ 3/48	3
6/15/48	Embryonic	6/18/48	....	5/19/48	6
6/21/48	Pla. Scar	6/18/48?	....	5/19/48	5
6/25/48	Embryonic	7/ 9/48	....	6/ 9/48	3
8/ 1/48	Nest	....	....	....	4
8/ 5/48	Embryonic	8/10/48	....	7/11/48	5
8/ 6/48	Embryonic	9/ 2/48	....	8/ 1/48	6
8/11/48	Embryonic	9/ 4/48	....	8/ 6/48	7

Number of litters—31 Litters average size—5.6

Reference to table 4 indicates that the dates of birth for most litters fell in March and May. After the large production in May a few birth dates were spread over the rest of the summer. Table 3 shows that between April 1 and August 11 seventeen females were autopsied. Fourteen of these were either pregnant or lactating at the time of autopsy. Discounting four rabbits in April which were in their first pregnancies and two juveniles in July and August which were in their first pregnancies, eight of the remaining eleven were both pregnant and lactating at the same time.

The above data suggest an extremely rapid reproductive rate for the first four months of the breeding season and strongly indicate that the majority of cottontails have three litters during this time (by the last of June). A good many cottontails have another litter after June 30. Judging from these data, it seems likely that an average female will produce at least three litters of five rabbits per litter during the breeding season and possibly more.

Breeding in the first summer.—Records of breeding cottontails in their first summer are not common. Cooley (1946) reported two such cases during an intensive six-year study of the Mearns cottontail in Michigan, both records appearing in 1942. Hendrickson (1947) reported one such case for a Mearns cottontail in Iowa. As far as is known, these are the only accounts of first season breedings on record. Of the specimens collected for the present study, two had bred in their first summer.

Rabbit No. 90 was killed on July 6, 1948. This rabbit weighed two pounds and three ounces. The presence of large ridges of epiphyseal cartilage on the humeri definitely classified it as a young of the year (Hale, 1947). The rabbit had recently ovulated as was evident by the presence of large corpora lutea in the ovaries (fig. 8). Ovulation had been too recent to diagnose pregnancy, but the fact that this rabbit had ovulated proved it was physiologically capable of reproduction.

Rabbit No. 96 was also classified as a young of the year by the presence of epiphyseal cartilage. This rabbit, which was killed on August 11, weighed two pounds and two ounces. It had recently ovulated and contained seven uterine swellings (four in one horn and three in the other). Only two of the seven swellings contained visible embryos, but they were so small (2 mm) that the others may have been missed.

SUMMARY

An account of the reproduction of the Cottontail rabbit in Illinois is herein offered for the first time. Mating behavior is described from actual observation. The breeding cycle of both male and female rabbits is demonstrated with photo-micrographs of testis and ovaries sections, and is supported by actual field observation of nests and the recording of pregnant females from collections. Descriptions and accounts are also offered of resorption, lactation, factors controlling rabbit reproduction, raising of young, growth and behavior of young, rate of reproduction, and accounts of rabbits breeding in their first year.

CONCLUSIONS

The complete courtship and mating of cottontails is herein recorded for the first time as far as is known.

Male gonads begin to develop as early as mid-January, but actual breeding condition, as determined by the numbers of sperm cells in epididimides, is not attained until the middle of February.

The starting date of the cottontail breeding season is largely dependent on the physiological and/or the psychological condition of females because male gonads are fully developed two weeks or so prior to actual fertile breeding.

The best criterion of male and female breeding condition is the physiological condition of the gonads as determined by micro-examination. Macro-examination, including weights and measurements of gonads, are often unreliable.

The breeding season for 1948 in central Illinois started during the last week in February, but did not reach full scale proportions until the first two weeks in March.

There is practically no evidence that resorption of embryos in cottontails is caused by somatic starvation due to excess lactation. Partial resorption (part of the embryos) sometimes occurs, but is most likely caused from other factors than somatic starvation.

Cottontails suckle their young from 16 to 25 days and possibly longer.

There are probably several external stimuli which control the length of the rabbit breeding season, the most important of which appears to be some component of green vegetation.

Female cottontails produce an average of three or more litters per year and average 5.6 young per litter as determined by data on 31 litters for 1948.

Nestling cottontails are nursed once, or not more than twice, during every 24-hour period.

Cottontails are covered with fine hair and can crawl at birth. Their eyes open between the 5th and 8th days, and they leave the nest on the 14th to the 16th day. While in the nest they gain from 2 to 5 grams daily.

No accurate method could be devised to age young rabbits although the length of hind foot appeared to be the most reliable of several criteria tried.

Young cottontails acquired intolerance towards one another at about 7 weeks of age.

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Life History Notes on the Eastern Chipmunk, Tamias striatus lysteri (Richardson), in Central New York

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The eastern chipmunk is widely distributed and known to many people. In spite of its abundance, some aspects of its life have not been fully recorded. Allen (1938) made a comprehensive investigation of this species, yet she emphasized the need for further research.

In June 1949 a study of the eastern chipmunk was initiated at Ithaca, New York, to determine its home range and the importance of territoriality. Incidental to the home range data, live-trapping operations provided considerable information on reproduction, sex ratios, survival, food, molt, and age determination. The present report deals with these life history aspects other than home range and territoriality.

Two hundred and thirty-nine chipmunks were live-trapped in the vicinity of Beebe Lake on the Cornell University campus. Many individuals were frequently retrapped during the period June 14, 1949 to July 15, 1950. A description of the study area, trapping techniques, and methods of marking has been given elsewhere (Yerger, 1953). Wihin a seven mile radius of Ithaca a series of 42 specimens was collected with guns and steel traps, or were found dead on highways and in the woods. Several observations are recorded of a litter of chipmunks born in captivity on August 8, 1949. All skeletal material used in age determination studies was cleaned by dermestid beetles.

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Reproduction

The duration of the mating season of the chipmunk in the Middle West has been stated by Condrin (1936), Schooley (1934), and Burt (1940) to extend from late March through April, and from July to August. However, Condrin collected a few pregnant females as late as October. Seton (1929) indicated that mating occurred in Connecticut in late March and April, and in Pennsylvania about the middle of June, for he cited a litter which apparently was born about July 15. In a study near Ithaca, Smith (1942) found two breeding seasons which correspond closely to the dates determined in the present study. These previous investigations have established the fact that the chipmunk, at least in the northern part of its range, has two breeding periods a year, one in spring and a second in summer.

Estrous period.—From the examination of both live and dead specimens, and by counting back 31 days (the gestation period) from known dates of

birth, the records of Allen (1938) and those from the present study show that females are in heat during the approximate period March 17 to April 7 in central New York. The summer estrous lasts from about June 19 to July 10. A female was considered to be in breeding condition when the vaginal orifice was unmistakably swollen and inflamed. It is possible that a few females may be in heat as late as mid-August, but it is believed that these are individuals which were born in early spring and matured the same year (see Age at maturity). This might account for scattered reports in the literature where young chipmunks have been seen as late as October.

Breeding season of males.—Adult males have been reported to be sexually active as early as the last half of February (Condrin, 1936; Allen, 1938). All adult males captured after March 18 (the earliest trapping period in 1950) had fully developed descended testes. No diminution in size was noted until the early part of August when they gradually became smaller and withdrew into the body cavity. This evidence agrees with that of Blair (1942) and Smith (1942). By the end of September or early October the testes are no longer visible externally. Earlier naturalists observed the great activity and excitement which chipmunks display in the autumn and mistakenly concluded that this was the rutting season. Rhoads (1903) even mentioned the possibility that females were newly pregnant when entering their winter sleep. The recession of the males' sexual powers in late summer invalidates this idea.

Dates of birth.—A female captured on April 18, 1950 had given birth within the previous day or two. Another was carrying full-term embryos on this same date. A pregnant female at full term was caught and released on April 23. Nursing females were frequently captured after April 21; at least 22 such individuals were recorded prior to May 7. Judging from the small size of several young captured in late June, it seems likely that a few litters are not born before the middle of May. The birth period of the first or spring litters consequently extends from about April 16 to May 10 in central New York.

The earliest date for a summer litter is July 21 (Allen, 1938). This agrees closely with the earliest observed date of estrous (June 19) in the present study. Another of the litters raised by Allen was born August 8, the same date that a captive female gave birth to a litter during the present study. Several pregnant females were trapped as late as August 8. A young chipmunk taken by W. J. Hamilton, Jr. on November 5, 1949 was estimated to be from 45 to 55 days old on the basis of teeth and skeletal characteristics, and had evidently been born about the middle of September, an exceptionally late date. Most second or summer litters are born between July 20 and August 10.

Number of young.—Examination of thirteen specimens (two embryo counts and eleven placental scar counts) showed a range of from one to six young, the average being four. The litter born in captivity consisted of three individuals. The literature indicates that chipmunks may produce from one to eight young, although four or five is the usual number.

Age at maturity.—There appears to be some disagreement as to the age when chipmunks attain sexual maturity. Burt (1940) found young from spring litters breeding later in the same year. Allen (1938) gave one account

of a small chipmunk, possibly from a fall litter, breeding twice in the following year, but the age of this animal was not definitely established. These two accounts suggest that females may mature at approximately three and seven months for spring and summer litters respectively. On the other hand, Manville (1949) doubted that either sex bred before the age of one year, at least in the Huron Mountain region of the Upper Peninsula of Michigan. Schooley (1934) believed that young females born in the spring and summer of one year would breed in the July cycle of the following year. He further stated that few year old males had scrotal testes during the breeding season.

In the present study, seven young females born in the spring of 1949 were captured and marked. Three of these were recaptured in the fall but were not breeding. The same three individuals were caught again the following April, May, and June, but only one was nursing. However, there is indirect evidence to show that some females breed at the approximate age of two and one-half or three months. Two pregnant females collected on Turkey Hill, four miles east of Ithaca, on July 30, 1949 were found to be young of the year, on the basis of tooth and skeletal characteristics. These animals were presumably born in mid-April.

Of the twenty females born and marked in the fall of 1949, 12 were recaptured the following spring, but only one was nursing a litter. This animal was later killed by an automobile on the Forest Home Road and found to possess four placental scars.

Males born in the spring showed no development of the testes during the summer months. In the spring of 1950, four of the eleven males marked the previous spring were recaptured, and in each case the testes were greatly enlarged and fully descended. In the fall of 1949, 15 young males from summer litters were marked. Between March 28 and July 10, 1950, only five of these had been recaptured, all of which had scrotal testes. In two cases the testes were as large as those in older adult males; in the others, they were slightly enlarged.

This study indicates that a few female chipmunks from spring litters mature at the age of three months, and a few from summer litters may mature at seven months. The majority of females probably mature at the age of one year. Males from spring litters attain sexual maturity at the age of one year, while those born in summer litters mature at seven or eight months of age.

Number of litters.—Although nearly all recent workers agree that the chipmunk has two breeding periods a year, some doubt still exists as to the number of litters which a female can produce in a year. The problem of which age groups comprise the breeding population in spring and summer is also in question. Allen (1938), Condrin (1936), and Burt (1940) stated that two broods a year may be produced by the same female. However, Schooley (1934) concluded that the breeding individuals in the July cycle included old females which had not bred in the spring and young females born the previous summer.

At least three females were in the final stages of nursing a spring litter when first captured in June, 1949 and were nursing a second litter when recaptured later in the season. There were several other records of females which bred during the summer estrous, but since the original captures were made in

early July, it was impossible to determine with certainty whether these animals had bred previously the same year.

These data verify previous observations that it is not unusual for a female to give birth to two litters a year. Consequently, the spring breeding population consists of old females, yearlings, and a few eight month old animals born the preceding summer. The summer breeding population consists of old females which may or may not have bred in the spring, yearlings, and a few young from spring litters which matured at the early age of three months.

Age of young at emergence.—Many authors have noted that the young appear above ground about one month after birth. In this study the first young chipmunks to be trapped in September, 1949 and in June, 1950 were weighed and measured. The smallest animal weighed 39.9 grams, and six others ranged from 41.7 to 50.0 grams. A comparison of these weights with those of young chipmunks raised in captivity indicates that, in all probability, these wild-trapped animals were in their fifth and sixth weeks.

Courtship behavior.—An observation of three chipmunks was made on the morning of June 14, 1949, at the beginning of the second estrous cycle. A female chipmunk had been feeding on the ground, but jumped on a log when she observed my presence. A male soon approached from the rear and began gently to nose the rump of the female, whereupon he was immediately chased away. The male repeated this approach several times, finally rubbing his nose along the neck of the female, but again was put to flight by the aroused animal. He took a position several feet away, crouched low, and slowly waved his tail back and forth in cat-like fashion. At this moment another male appeared on the scene, and was promptly chased up the nearest tree by the first male, who returned to his former position. By this time the female had resumed her feeding activities. She displayed no further interest even though she had appeared to be in a receptive mood when the male rubbed the side of her neck and body. This observation was concluded when the first male chased the second away from the area.

Sex ratio.—Few investigators have handled sufficiently large numbers of chipmunks to establish an accurate picture of the sex ratio. Burt (1940) marked 106 animals over a three year period and found a 60 to 40 per cent ratio with males predominating. Blair (1942) observed a fairly even number of males and females (51.3 per cent males to 48.7 per cent females) among 154 chipmunks in northern Michigan. Smith (1942) marked 60 animals of which 55 per cent were females and 45 per cent males. Linduska (1950) found that males comprised only 40 per cent of the 333 animals captured over a three year period, and that the situation was essentially the same when the ratio was considered for each year separately.

Table 1 shows the sex ratios for young and adult chipmunks in the years 1949 and 1950, as well as the ratio for all classes during the entire period of study. The figures for adults in 1950 include those animals that were marked in 1949 and recaptured in 1950 as well as the new individuals that were marked in the latter year. It is evident that the sex ratio shows a predominance of females (56.44 per cent). The spring litter of 1949 is an exception, but the number of animals marked in that group is probably too small to provide an

TABLE 1.—Sex ratios of the eastern chipmunk

	Number of animals		Ratio in per cent	
	Male	Female	Male	Female
Spring young 1949	11	7	61.11	38.89
Summer young 1949	15	20	42.87	57.13
Spring young 1950	12	25	32.43	67.57
Adults 1949	34	51	40.00	60.00
Adults 1950	37	50	42.53	57.57
All age classes 1949-50	88	114	43.56	56.44

accurate ratio. During the course of the study, 42 dead animals were examined. Most of these were shot, a few were trapped, and several were found on the highway. The ratio in this group was 64.28 per cent females to 35.72 per cent males.

In his work on the fox squirrel in Michigan, Allen (1943) has shown that increasing populations have been associated with a predominance of females. Perhaps the high chipmunk populations in the Beebe Lake area can be correlated with this uneven sex ratio.

WINTER SURVIVAL

Linduska (1950) appears to have given the only information to date on the percentage of chipmunks surviving from one year to the next. In his three year study he found that only about ten per cent of the animals marked in any given year were recaptured the following year. Since there was little evidence of chipmunks moving any great distance, he concluded that the annual population turnover was due mainly to high mortality.

The percentage of survival in the present study was considerably higher. Of the 117 chipmunks marked on the study area in 1949, 53 were recaptured in 1950, or a 45 per cent survival. If we exclude the young from summer litters in 1949 from the above figures, then 84 animals were marked and 47 of these recaptured in 1950, a survival rate of 56 per cent. The reasons for the great difference in survival between Linduska's and the present study can only be surmised. Perhaps predation was less important in the Beebe Lake area, although two species of weasels were known to be present.

Apparently there have been no data published on the percentage of young chipmunks surviving over their first winter. Although the records obtained in this study are limited in number, they at least provide an estimate of the rate of survival from the first to the second summer.

Fifty-three young were captured and marked in 1949. Between March 28 and July 10, 1950, twenty-four of these animals were recaptured one or more times, a survival of approximately 45 per cent. The survival of young from spring litters was 39 per cent (18 chipmunks marked and seven recaptured), and for summer young, 49 per cent (35 marked and 17 recaptured). Although no extensive movement of chipmunks was found during the study, it is possible that some of the young moved out of the area, in which case the percentage of actual survival would be higher than the above calculation. It is interesting to note that a greater percentage of females survived than males, 56 to 35 per

cent. Geiser (1923) has shown that this same condition prevails in many diverse groups of animals.

FOOD

The food habits of the chipmunk have been summarized by Seton (1929), Howell (1929), and Allen (1938). As with many species of wild animals, availability seems to be the important factor which determines the kind of food that chipmunks will consume in any given area. Additional information was obtained in this study of the food habits of this animal in the Ithaca region.

During the latter part of June when sweet cherries (*Prunus Avium*) were at their height, chipmunks were observed making frequent trips between the trees and their burrows, their cheek pouches crammed with cherry pits. In the middle of July, choke cherries (*Prunus virginiana*) were one of the favored foods, and chipmunks and robins were seen feeding within a few feet of each other on the same branch. Cherry pits were frequently found in the traps after the chipmunks had removed them from their cheek pouches.

Other June foods consisted of the underground corms of the yellow adder's tongue or dogtooth violet (*Erythronium americanum*). Chipmunks were observed digging these corms out of the ground and eagerly devouring them. On several occasions these corms were found in the traps, having been emptied from the cheek pouches by the captive animal. One chipmunk was observed eating the seeds from the fruiting heads of wild geranium or wild cranesbill (*Geranium maculatum*). Maple samaras were frequently found scattered about chipmunk holes and stumps during the spring months.

Only two of the animals which were shot had food in the pouches. One female was carrying 48 cherry pits. The other, a nursing female, had a varied array of items: one snail (*Ventridens ligerus*), one slug (*Philomyscus* sp.), three earthworms (*Lumbricus terrestris*), one lepidopterous larva, one wood frog (*Rana sylvatica*), and fragments of acorns. This is one of the few records of a chipmunk preying upon frogs. Several others have been mentioned by Seton (1929), and recently a similar incident was described by Hesterberg (1950).

Twenty chipmunk stomachs were examined. One of these was empty, and two others contained mast only. This material formed a large proportion of the contents in six others. The seeds of aromatic wintergreen (*Gaultheria procumbens*) were found in three stomachs taken June 16 and 17 at Ringwood, seven miles east of Ithaca. Seeds of blackberries (*Rubus* sp.) were abundant in six stomachs, collected from late July to the middle of August on Turkey Hill, about four miles east of Ithaca. Slugs (*Philomyscus* sp.) occurred in three stomachs taken between August 12 and September 7. The remains of a salamander were found in the stomach of a juvenile chipmunk killed on August 27. Only the feet were recognizable and could not be identified as to species, although it probably was *Plethodon cinereus*. Earthworms occurred in four stomachs taken at different times throughout the summer. Insect remains were common, and were present in 12 of the 19 stomachs which contained food. Dipterous and lepidopterous larvae were identified, and adult insects were also found. The carnivorous habits of these rodents have

long been known, but the extent to which they feed on animal matter is little appreciated.

MOLT

Little information has been published on the molt of the chipmunk. Howell (1929) stated that there was apparently one annual molt which usually occurred in June or July. Bole and Moulthrop (1942) concluded that there were two molts each year, and described a distinct summer and winter pelage. They found that *Tamias striatus rufescens* acquired the summer pelage during late June and early July. The second molt began in September and was completed by mid-October. By late spring, this winter pelage was faded and worn. They also stated that the summer molt of *Tamias striatus lysteri* in the Georgian Bay area occurs in August.

The present evidence was obtained from the skins of 22 chipmunks (16 adults and 6 juveniles) killed between June 16 and September 7, 1949, and from field records of live-trapped, marked animals during the period June 14, 1949 to July 15, 1950. The problem is considerably complicated by the fact that juveniles and adults do not molt at the same time. Also, in many species of mammals, the molt of the females which breed in the spring is delayed as much as two or three months in contrast with males and non-breeding females. The progress of the molt in the chipmunk generally follows the sequence described by Nelson (1945) for the spring molt of the red squirrel.

In young chipmunks born in April and May, the first molt begins in late June and is completed before the end of August. Young born in August begin molting about the middle of October and probably complete the process by the time they disappear for the winter in early December. Two of the latter group were marked during the first week of October and recaptured on November 13. The clipped area had grown in completely and the pelage resembled that of an adult. Both animals were remarked, and one was observed the following spring on May 20 with plainly visible marks. Other chipmunks from summer litters that were marked in the fall were not recaptured until the following March and April when all areas of clipped fur had been replaced by a new growth of hair.

The molting period in adults is not well defined. The lack of late fall and winter specimens and observations leaves an incomplete record. Most of the evidence supports a two molt theory, but apparently there are exceptions. Specimens collected from June to September demonstrate with certainty that adults molt sometime between late June and the end of August. Field records of marked chipmunks with clipped fur confirm this, but in rare cases the molt appears to begin as early as the middle of May. Evidence for a second molt is furnished by at least seven chipmunks which were captured and marked by fur clipping in August, September, and October, and recaptured the following March, April, and May. A new growth of fur had obliterated the original marking during the intervening period, probably in late fall and early winter. However, in one case, growth of new hair was observed on the rump of one individual on March 28, indicating that occasionally the winter molt may not be completed until early spring.

In contrast to the above data, two field records appear to support the one

molt hypothesis. One female was marked in mid-August when the summer molt appeared to be complete. This same animal was observed in mid-June of the following year and captured two weeks later. On both occasions the clipped mark was still evident. In the other example, an adult male was marked on October 16, recaptured in March and May, and observed in June. The two marks (nape and flank) were visible on all occasions. In the latter case it is possible that the animal had already completed the fall molt when it was originally captured in October, but neither of these two individuals seem to conform with the two molt pattern suggested by the other examples.

In summary, my data generally substantiate those of Bole and Moulthrop (1942), but the dates of these molts apparently vary in different localities. In central New York one molt occurs in late spring and early summer; the second in late fall or early winter, but possibly extends into late winter in some individuals.

HIBERNATION AND AESTIVATION

Trapping operations were suspended from the middle of November to the end of March. Nevertheless, chipmunks were observed on several occasions during December, January, and early March. Although the chipmunk was called a hibernator by the early naturalists, it has been observed during the winter in nearly all parts of its range, and cannot be placed in the same category as the woodchuck and jumping mouse.

Many theories have been advanced to account for the scarcity of chipmunks during late summer. Several persons have suggested a period of aestivation; others that reproductive duties have been responsible for the lessened activity. Schooley (1934) concluded that the males were relatively inactive, and that the females were busy foraging and therefore made few vocal sounds. Hunting and trapping efforts during the month of August corroborate Schooley's (1934) conclusion. Females outnumbered the males two to one among the twelve specimens that were shot. During this month an equal number of males and females were captured, but the total number of captures for males was only two-thirds of the number for females. Field records also show that chipmunks were rarely heard calling during the month. The summer disappearance of chipmunks is a misstatement of fact. Careful observations indicate that they are active throughout the summer, but that they are much less conspicuous than in the spring and fall months.

AGE DETERMINATION BY TOOTH AND BONE CHARACTERISTICS

Among the many methods used to determine the age of mammals, the condition of the teeth and ossification of the long bones are among the easiest techniques to employ. From a series of 36 chipmunk skeletons collected by Hamilton and the author, an attempt was made to find one or more characteristics which could be used to determine the approximate age of the animal. A summary of the tooth and skeletal characteristics of chipmunks from the age of one month to one year is given in Table 2.

Dentition.—The development of the dentition from birth to 70 days has been described by Allen (1938). This remains the best method for aging an

TABLE 2.—Tooth and skeletal characteristics of the eastern chipmunk at various ages

Structure	1 month	2 months	3-5 months	9-11 months	One year and older
Skull:					
Teeth	Temporary premolars; last molar lacking in lower jaw.	Permanent premolars developing.	Complete permanent dentition; sharp cusps and crests.	Moderately worn; cusps and crests low.	Well worn; cusps and crests barely evident.
Temporal ridge	Absent.	Absent or chalky outline only.	Weak to moderate development.	Moderate to complete development.	Complete development.
Lambdoidal crest	Absent or weakly developed.	Moderately developed.	Well developed.	Well developed.	Well developed.
Innominate bones (sutures)	Distinct.	Scarcely visible.	Not visible.	Not visible.	Not visible.
Epiphysis of long bones	Spongy; cartilage groove prominent.	Cartilage groove present.	Groove less distinct but visible.	Line marks location of indistinct groove; dark reticulations developing on femur and tibia.	No groove or line visible; reticulations present.

animal less than two and one-half months old. However, once a complete set of permanent teeth are present, then the amount of wear can be used to place the animal in an approximate age group only. From three to five months, the premolar and molars have high crowns with prominent cusps and sharp ridges. A progressive wearing down of these features follows, so that by the time the animal is nine to eleven months old the ridges and crests are lower and more rounded. The crowns of the teeth are low in year old animals; all the cusps and ridges have practically disappeared except for the folds of enamel which are still evident. In very old animals the teeth are extremely low crowned and show scarcely any remnants of crests or ridges.

Skull.—Certain features of the chipmunk skull change with growth, but it is extremely difficult to determine age by this means alone. Sutures separating various elements of the skull are not helpful. Some sutures remain quite prominent throughout life (those separating frontal and parietal bones, frontal and premaxillaries), while others disappear relatively early. The suture separating the two parietals generally is indistinct after three to five months. The lambdoidal crest is not evident on skulls of chipmunks less than one month old, but in the second and third months it develops rapidly. The temporal ridge is absent during the first two months of life. It gradually develops during the third and fourth months, first as a chalky outline, and later as a weak ridge. By the tenth month it is well developed, and is found in practically all adult chipmunks.

Long bones.—The changes which occur in the epiphyseal regions of the humerus, femur, and tibia are quite similar; therefore, the following description will apply to all three. In one month old specimens, the epiphyseal cartilage is soft, has a sponge-like structure, and is separated from the diaphysis by a prominent, well-defined groove. At three to four months, the bone is capped by hard osseous material, but a prominent groove remains, separating the shaft from the epiphysis. At the age of nine to ten months, the epiphysis is smaller and the cartilage groove is present only as a line. At eleven months this line is scarcely discernible. A series of dark, lengthwise reticulations begins to appear in the concave area which lies between the condyles of the femur, and also on the head of this bone. These marks are also present to a lesser extent on the proximal end of the tibia. In chipmunks one year old or more, the epiphysis is closed and neither a cartilage groove nor a line is visible (A few twelve month old specimens may show the slightest trace of a line). The dark reticulations are plainly visible.

Innominate bone.—In young mammals, the three elements of the innominate bone are distinct, and separated by prominent sutures. This condition is found in the chipmunk for about forty days only. The sutures may be vaguely discernible until the end of the second month, but fusion of the three elements is complete after that length of time.

LONGEVITY

Few records are available to indicate the maximum age attained by chipmunks in the wild. Burt (1940) found one of the 106 animals which he

marked to be three years old, and several that were two. Linduska (1950) marked 141 individuals in 1940, and one of these was three years old when last handled in 1942. Allen (1938) reported captive animals which lived five and eight years, but estimated the average length of life for wild chipmunks to be two or three seasons.

Although the data from the present study provide little information on longevity, the results of live-trapping in the study area over the next few years should yield significant knowledge since many marked animals of known age are now at large. At the conclusion of this study, at least eleven chipmunks were known to be at least two years old.

SUMMARY

Data collected incidental to a home range and territoriality study of the eastern chipmunk are presented as a contribution to our knowledge of the life history of this species. Field work was conducted from June 14, 1949 to July 15, 1950 at Ithaca, New York.

Estrous periods of the chipmunk extend from March 17 to April 7, and from June 19 to July 10, with some exceptions. Males are in breeding condition from mid-February to August. The majority of first or spring litters are born from April 16 to May 10; the second or summer litters from July 21 to August 15. Most female chipmunks become sexually mature at the age of one year; a few of those born in spring may mature at about three months of age, and a few born in summer litters mature at seven or eight months. Males born in spring mature at one year of age; most males from summer litters are in breeding condition the following spring, at an age of seven or eight months. A female may bear two litters a year. An observation of courtship behavior is described.

The sex ratio shows a predominance of females, 56.44 to 43.56 per cent. Forty-five per cent of the animals marked in 1949 were recaptured in 1950. The percentage of young females surviving over the winter appears to be higher than for males. The percentage of winter survival for young is about 39 per cent for spring litters and 49 per cent for summer litters of the preceding year.

Analysis of stomach and cheek pouch contents reveals that the diet changes seasonally. Animal matter, especially insects, forms a large part of the chipmunk's food. Uncommon food items reported in this study are a salamander and a frog.

Juvenile chipmunks begin their first molt at approximately two months of age. Adults appear to molt in late spring to early summer, and again in late fall to early winter.

A few reports of chipmunk activity are recorded during the winter of 1949-1950. Chipmunks are inconspicuous during July and August, but a state of aestivation is quite improbable. Males are relatively inactive at this time, and females are engaged in reproductive duties.

Tooth characters are the best criteria for determining the age of chipmunks less than three months old. The condition of the cartilage groove in the epiphyseal region of the humerus, femur, and tibia can be used as an age criterion during the first year. The lambdoidal crest develops in the second

and third months. The temporal ridge develops from the third to the tenth month, and is characteristic of adult chipmunks.

No longevity records exceeding two years could be established during the course of the study, but future trapping in the study area may reveal additional data.

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Southwestern Exotic Felids

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The feline fauna of the major portion of the United States is poor in number of species, for only the bobcat, Canada lynx, and cougar are its normal members. South of our boundary several other species occur, so that Central and South America have a richer share of this interesting family. Four of these southern species at times cross or have crossed our borders, and are thus to be considered as rare regular or occasional members of the fauna of the United States.

Due to the nature of their habits these four members of the genus *Felis*—the jaguar, the ocelot, the margay, the jaguarundi or eyra—are rarely seen. When seen, they are usually shot on sight, but their very rarity makes them hunters' trophies, so that only seldom does the mammalogist obtain a specimen. Indeed, the paucity of published records would indicate that only rarely does he hear of them. For this reason, it seems pertinent to bring some of the more recent records together, and to add a new one.

Jaguar

This beautiful spotted "tiger" is perhaps the widest distributed and best-known of these exotic cats within our borders. Anthony (1928) lists *Felis onca* as occurring in Texas, New Mexico, and Arizona. Nelson and Goldman (1933) amplify this to cite records from California, northern New Mexico, well north in Texas, and from the Grand Canyon southward in Arizona. Seton (1920) refers to a book by R. B. Cage (1843, *Rocky Mountain Life*) in which is reported an encounter with a spotted cat in Colorado. Seton thinks that the beast referred to is the jaguar or ocelot.

Merriam (1919) and Strong (1926) cite the former occurrence of the jaguar in California on the basis of Indian records. Strong gives the Kammei Indian name for this animal as *tu' kwat*. The last one known was killed at Palm Springs about 1860, when it attacked an Indian wearing mule deer antlers and skin.

Seton (1937) gives two additional records of the occurrence of this species in California. One of these relates to the finding of a pair of jaguars and their two young in Tejon Pass in the Tehachapi Mountains. His map shows these records, plus three others which are considered doubtful.

Nelson and Goldman (1933) describe the subspecies occurring "north to central Texas" as *F. o. veraecrucis*. Bailey (1905) says that the jaguar formerly occupied nearly the whole of Texas, but is now extremely rare. It was so considered even in 1879, but records as late as 1902 and 1903 are given. Seton (1937) gives several additional records from 1845 to 1910. These are also shown on his map. Taylor (1947) lists one killed 30 January, 1946, at San Benito, Cameron County, Texas. He says there are no other recent records. Taylor and Davis (1947) state that the species was killed off because of its stock-killing habits, and has been extinct in Texas for more than twenty years (with the above noted exception).

Bailey (1931) says that the few records from New Mexico are generally supposed to be wanderers from over the Mexican border, but that he thinks they are native. They were first recorded from New Mexico by Coronado in 1540, but Baily gives no records later than 1904 or 1905. Seton (1937) adds only a record at Santa Fe in 1825, and this may be doubtful. If true, it is of great interest due to the fact that this jaguar was a man-killer. He gives an account of this occurrence. Hill (1942), writing on the mammals of the northeastern part of the state, says a jaguar was killed near Springer (Colfax County) "some years ago," and none has been seen since. Halloran (1946) did not secure any records of the jaguar in the San Andres mountains from 1941 to 1944, although he suspects occasional wanderers occur.

Schufeldt (1921) relates the circumstances surrounding the killing of a jaguar in the Rincon Mountains near Tucson, Arizona on March 16, 1902. A letter from Herbert Brown of Yuma is quoted. In this letter Brown tells of several members of this species killed "within the last few years" in Arizona. One of these was in the Chiricahuas, one in the Baboquivaris, and one near Globe. Another was seen on 9 March, 1902, in the Tortolito Mountains. He had also seen several skins taken by the Papago Indians in the mountains southwest of Tucson (Baboquivaris, Sierritas, Cerro Colorados, other, ?). He also recalls several other cases when it was taken, but does not remember details. Schufeldt (1921) says that he published his 1902 record as the first account of the jaguar's occurrence in Arizona. Musgrave (1921) also discusses the jaguar in Arizona. Seton (1937) lists several additional records of this cat in Arizona.

Nelson and Goldman (1933) in their revision of the jaguars, list the range of *Felis onca arizonensis* Goldman as the mountainous parts of eastern Arizona north to the Grand Canyon, the southern half of New Mexico, and northeast Sonora, formerly to southeastern California. The type locality is Cibecue, Navajo County, Arizona; the date of collection 12 April, 1924, and the type specimen is deposited in the National Museum (Poole and Schantz, 1942). Other specimens seen were from Nogales (20 mi. west), 1 skull; Greaterville, 2; Sonora, (Sierra Madre, west of Casas Grandes, Chihuahua), 1 skull. Nichol (1936) says "El Tigre" is of rare occurrence and is a migrant visitor from Mexico. Cahalane (1939) cites the jaguar as occurring in the Chiricahua Mountains. His only record with dates is a jaguar killed in January, 1912, near the Chiricahua National Monument. The skin is in the University of Arizona collections. It was seven feet, nine inches long.

The New Record.—A more recent record of the jaguar in Arizona was secured in November, 1949. As reported in the Arizona Star (Tucson, Arizona) for 15 November, 1949, Walter Noon, Sr., and Walter Noon, Jr., were deer hunting in the Cerro Colorado region near Arivaca (Pima County). They were dressing out a buck when the jaguar was seen about twenty feet away. They shot the beast, killing it at once. I wrote to Mr. Noon, Sr., at Nogales, asking for the skull of the jaguar. His reply stated that one of the shots destroyed the lower jaw and part of the upper jaw, so the skull was not saved. The Star account shows a picture of the animal, which would appear to be about five to six feet in total length. It is my understanding that Mr. Noon has retained this skin as a trophy.

OCELOT

Felis pardalis is also an occasional visitor from over the line. Anthony (1928) states that it crosses into the United States only in Texas. Bailey (1905) says that early records carried their range into Louisiana and Arkansas but that they were probably not found at the time of his writing in the states outside of Texas. He gave many records, indicating that in southern Texas this cat was not rare.

Taylor and Davis (1947) give the former distribution in Texas as including the eastern, middle, and southern parts of the state. It is now rare, and restricted to the extreme southern section, south of a line between Eagle Pass and Corpus Christi. It is interesting and gratifying to note that, "In view of the attractiveness and value of the ocelot, government hunters are instructed to release any that may be caught accidentally." Davis (1951) records a 4'6", 45 pound ocelot taken in early December, 1950, two and one-half miles north of Hedley, Donley County, Texas. Another was seen near Clarenden in mid-December. These records are 350 miles north of the previous northernmost Texas records in Kerr County. Seton (1937) lists it as occurring at that time only in Texas, although it had formerly been taken in Louisiana and Arkansas, the type locality of *albescens* Pucheran (Goldman, 1943).

Goldman revises the ocelots, and lists the subspecies *sonoriensis* Goldman as occurring from the west slopes of the Sierra Madre from southern Sonora northward to southeastern Arizona, formerly west to Fort Verde (Yavapai County), Arizona. He had examined a specimen from Fort Verde, said to be in the American Museum of Natural History. These two subspecies appear to intergrade, but this must be in Mexico, for Goldman does not mention New Mexico in the ranges. Bailey (1931) does not mention the ocelot in New Mexico. The reason the ocelot is not known to occur in New Mexico seems to be explained by a statement by Goldman (1925). He says that the "range of *Felis pardalis*, transcontinental in tropical Central America, is split in southern Mexico by the great wedge formed by the Mexican highlands. From this point diverging branches extend northward along the Gulf slope to southern Texas [*albescens*], and along the Pacific coast to Sonora and Arizona [*sonoriensis*]." Goldman (1943) says "The subspecies *albescens* represents the northern limit of the ocelot east of the continental divide, which interposes a barrier between eastern and western northward extensions of the general range of the species in northern Mexico." The Mexican highlands continue on into New Mexico and northeastern Arizona (Atwood, 1940), thus excluding the ocelot from that region. Nichol (1936) refers to the ocelot, but adds no data except that it is rare in Arizona.

MARGAY

Goldman (1943) lists *Felis wiedii cooperi*, ssp. nov., the Texas margay, with type locality at Eagle Pass, Texas. This form is known only from the type locality, but probably occurs widely in northeastern Mexico. The type was taken in 1852, and appears to be the only specimen. Bailey (1905) does not refer to this species, but Taylor and Davis (1947) say that none has been collected in Texas since the middle of the last century (this is presumably the type).

JAGUARUNDI OR EYRA

Felis yaguarondi cacomitli Berlandier is another member of this genus whose range extends just to the International Border. Anthony (1928) lists it as occurring in the United States only in extreme southern Texas. Bailey (1905) believed that *cacomitli* would be found to be a subspecies of *yaguarondi* when enough Central and South American specimens are available. Charles O. Handley, Jr., of the National Museum, tells me that this is now the recognized nomenclature. Bailey refers to five specimens of this cat from Brownsville, Texas in the Biological Surveys Collection, and several live specimens from the Lower Rio Grande then in the National Zoological Park. Taylor and Davis (1947) say that this cat is known from the brush country of extreme southern Texas, at least from Cameron, Hidalgo, Starr, and Willacy Counties. They refer to it as the eyra, but this name, according to Anthony (1928), refers to the red phase. This subspecies ranges in Mexico east of the Plateau. To the west of the Plateau in Mexico *Felis yaguarondi tolteca* Thomas is found. As in the case of the ocelot, this may explain the lack of New Mexico records. Elimination of the brush in the Brownsville area will cause extirpation in the United States of this small (18 pound), secretive, and little known animal (Taylor and Davis, 1947). Seton (1937) shows the range in the United States to be restricted to extreme southern Texas.

Little (1938) records a sight record of this cat made in the Huachuca Mountains, in Santa Cruz County, Arizona, on 17 March, 1938. This is 15 miles north of the border. He had an excellent close-range sight of it as it loped away. His reference is to *Felis yaguarondi tolteca* Thomas, which is the subspecies found west of the Mexican plateau. This is the only reference to this species in Arizona, and appears to be the only record of the subspecies in the United States. It is, of course, poorly based.

OTHER SOUTHWEST FELIDS

To make this a full discussion of the Felidae in the Southwest, it is only necessary to add that one or another of the subspecies of *Felis concolor* Linné is to be found over the entire region in suitable habitat (Nelson and Goldman, 1929). The cougar is by no means rare in this region (Musgrave, 1926), and probably will continue to persist in its wilder parts despite the efforts of stock men, government predator control agents, and others to eradicate it. The same is true of *Lynx rufus* Schreber, the bobcat.

The species discussed in the present paper will probably also continue as residents of this area, though rare or occasional. The nature of the border country is such that it will be a great many poison baits away before these fine felids are all gone from this area.

SUMMARY

The range of four exotic members of the family Felidae that occur in the southwestern United States is given, and specific records listed.

One record of the jaguar in Arizona in 1949, not previously recorded in literature, is added.

An explanation of the non-occurrence of the ocelot in New Mexico, despite its occurrence in Texas and Arizona, is advanced. This holds that the extension of the Mexican highlands into New Mexico prevents this species

from occurring there, as it is split into eastern and western subspecies by the intrusion of the Mexican Plateau, and does not occur in the plateau country. The jaguarundi may also be excluded from New Mexico for this reason, for it is not uncommon in southern Texas, and there is one sight record for Arizona.

It is concluded that, due to the nature of the border country, these cats plus the cougar and bobcat will persist as a little-known, though perhaps fairly common, segment of the mammalian fauna.

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Breeding Behavior and Nesting of the Eastern Robin*

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The wide distribution, abundance, comparative tameness and accessibility of the robin, *Turdus migratorius*, has made it a popular subject for study. Farner (1945, 1949) has taken advantage of the large numbers banded to compute its mortality rates and longevity; Young (1951) has examined the territorial behavior, Speirs (1946) the movements, and there are innumerable short notes on various aspects of its life history. However, the only previous extensive study of the breeding behavior and nesting of the robin is that of Howell (1942).

This paper furnishes data to supplement those of Howell's, discusses the subject of mating behavior, and considers in detail the breeding success, the nesting season, and population dynamics.

The material was gathered during the spring and summer from 1947 to 1949 at Madison, Wisconsin. Two major study areas were used. The first, known as the Ho-Nee-Um area, is located in the University of Wisconsin Arboretum. It is a small (5.2 acres) park-like area, where arbor-vitae, *Thuja occidentalis*, furnished the main nesting cover. For a detailed description see Young (1949a, 1951). Many robins at Ho-Nee-Um were individually marked in connection with a concurrent territory study (Young 1951), and these marked birds were also watched for breeding behavior. Marked birds are herein referred to as M1, M12, etc. (♂), and 9F, 13F, etc. (♀). This study area was visited almost daily during the breeding season in each of the three years; the visits usually lasting from 2 to 3 hours, with a total of about 700 hours spent on the area. The second area used was the Forest Hills Cemetery at Madison, which was under observation mainly during 1948 and 1949. It was usually visited about 3 times a week, each visit lasting from 1 to 2 hours, for about 100 hours total.

The nests were ordinarily examined every other day. On a few unavoidable occasions longer lapses of time intervened, and at certain stages the nests were checked more frequently. Each visit to a nest was of as short a duration as possible (to determine the status) since intensive observation of incubation, brooding, and development of the young was not in the scope of the study.

Acknowledgment is due to Dr. John T. Emlen, Jr., who supervised the project, and to Dr. J. J. Hickey, for critical readings of preliminary reports on the study.

The Breeding Behavior

Territorial behavior, while an important part of breeding activity, has been separately discussed (Young 1951) for purposes of clarifying presentation. In

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life it is superimposed upon the epigamic behavior, and the robins switch from one activity to the other under the influence of various stimuli, so that territorial fighting and mating, or territorial fighting and nesting activities are carried on more or less simultaneously.

The subject of courtship and pair-formation has long created strong interest among ornithologists. Major contributions in the field have been made by Lack (1943), Armstrong (1947), Nice (1943), and Noble *et al.* (1938).

In the robin, the courtship and method of pair-formation does not appear to be conspicuous, and no definitive description can be given. An examination of the literature indicates that the Turdidae have been somewhat of a problem in this respect, no detailed and analyzed reports being available. The following paragraphs list such descriptions as were located, with comparison with the robin where applicable.

COURTSHIP FEEDING AND GAPING

Courtship feeding has been reported for the mistle thrush, *Turdus viscivorous*, (Boyd 1946), and for the blackbird, *T. merula*, by Manning (1946) and Chappell (1946). However, among the thrushes, it appears to be common only in the European robin, *Erithacus rubecula*. Observations on *T. migratorius* are inconclusive in this respect. Courtship feeding by this species has been reported by Brackbill (1944), who did not, however, see any food passed between the birds.

Another type of display possibly associated with pair formation is ceremonial gaping, in which the birds approach each other and touch, or nearly touch, widely opened bills. In this respect, Armstrong (*op. cit.*) says that various European thrushes have a vague yawning display. One pair of robins under observation by the author in 1946 was seen to engage in this display on several occasions (Fig. 1). However, these birds were already paired, and the gaping was noticed when they paused during sallies against the observer as they defended their nest. The interpretation at the time of observation was that it represented a type of substitution activity, *vide* Armstrong (*op. cit.*)

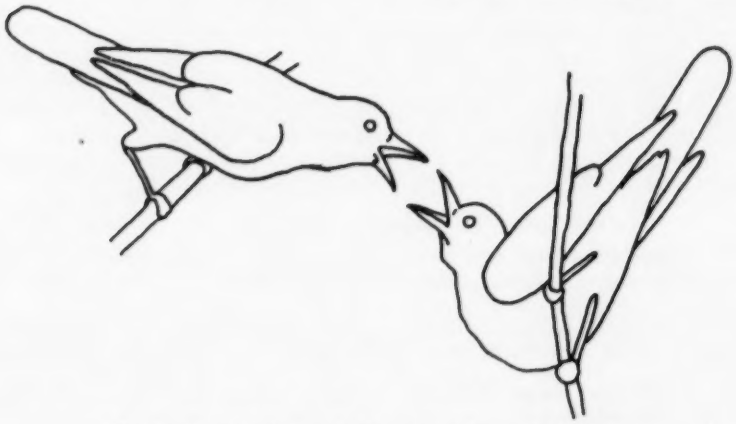

Fig. 1.—Gaping behavior of robin (copied from a field sketch)

Tinbergen (1939). Brackbill's (*op. cit.*) observation may refer to the same type of behavior.

During July, 1949, R. Nero, of Madison, observed robin behavior which seemed to be a combination of symbolic feeding and ceremonial gaping. In this case, which followed copulation, the male posed in front of the female and begged. She turned her head sideways and put her beak near his. The male then flew to the top of a building, the female following. Here the male distinctly squatted in front of the female and raised his head with open beak, in the manner of a young bird begging. The female did not respond, and there was no further display.

Records of male robins feeding females on the nest (Howell 1942) are presumably of long-paired birds, and courtship feeding as an initial step in pair formation does not appear to have been definitely observed in the robin.

SONG

Song has been frequently associated with avian mating behavior, and obviously plays an important role in the pair formation of some birds, *e.g.*, manakin, *Manacus* spp. (Chapman 1935) and prairie chicken, *Tympanuchus cupido* (Main 1937).

In the robin, two types of song were noted during the period of this work: the typical loud carolling song, and a subdued high-pitched *whisper song*. The latter often serves as a threat (Young 1951), and perhaps is generally indicative of an excited condition. No function, however, could be definitely assigned to the loud carolling song. The following observations suggest that it functions as an advertisement for a mate, but the subject needs considerably more study before more positive statements can be made.

During July of 1947, M12 suddenly came into loud song; he had previously been silent. Not resident on the study area, he abruptly shifted his activity to that region, moving restlessly from one territory to another and carolling vigorously. He elicited no noticeable response from males or females, and disappeared after two days of this behavior. Such activity could be interpreted as an advertisement for a mate. However, in this case, the mating status of M12 was not known prior to, or after, the period of song.

M1 came into loud song (1948) after the loss of his first mate; he had previously been singing very little. In this case he was successful in obtaining a new mate, and shortly stopped singing again. Yet other males, never heard to sing prolongedly, were successful in obtaining mates.

The closely related European blackbird seems to have similar song habits. Lack and Light (1941) found its song to be only "vaguely correlated with mating," and Heyder (1931) speaks of *sangfaul* blackbirds which bred successfully.

The territory of M1 was invaded in April of 1948, apparently by a mated pair. The male of this pair sang the loud carolling song for several days, and engaged in numerous contests with M1, until he permanently established himself in part of the territory. However, no *song duels* were ever observed between robins. Among the thrushes this apparently has been found only in the song thrush, *T. ericetorum*, by Siivonen (1939).

The carolling decreases after pair formation, but may be heard at any stage of the breeding cycle.

Generally speaking, the robins seemed able to maintain their territories with very little recourse to carolling as a *warning song*.

COPULATION

Litterdale (1944) described coition in the blackbird; it was not preceded or followed by display.

With the exception of Nero's (see preceding) observation, and one case of apparently atypical copulation (Young 1949b), no display by robins was noted prior to nor following the act, the male simply going to the female, mounting quickly, and then moving off without either bird displaying signs which could be interpreted as excitement. The males occasionally fanned their wings vigorously during copulation. The act was observed to take place both on the ground and on elevated places.

In April 1948 two females were noted in association with a single male; the females frequently squatting as though to invite copulation. The male bird did not respond over a period of five minutes, and was finally attacked and chased by one of the females.

On several occasions, aberrant, or at least non-functional copulation was noted. Some examples are listed below:

1. In August 1948 an immature robin was seen to mount an empty cigarette package, and make copulatory movements. It then picked up the package, dropped it, and once again went through copulatory movements on it.

2. In June 1949 one immature mounted another, and fanned its wings vigorously. The other bird sat quietly for the duration of the act (*ca.* 20 seconds) and the two then fed quietly together.

3. In July 1949 one immature mounted another which was sitting in a *Lonicera* bush. The bird which had been mounted called loudly, the notes being similar to those used in begging, and both flew away immediately after the act.

4. In June 1949 Mrs. F. Greeley of Madison saw a banded female robin trying to mount one of its own fledglings.

5. In April 1949 two robins, both apparently males, were fighting, when one of the birds seized the other by the nape, mounted, and fanned its wings. The other bird ran, they had another short fight, and then separated.

Aberrant sexual behavior has also been reported for the robin by Brackbill (1947).

OTHER DISPLAYS

Geyr (1933) mentions male blackbirds (*T. merula*) brawling over a female in the fashion of house sparrows, *Passer domesticus*. He also gives an incomplete account of *pair formation* in which one bird dropped its wings and quivered them, while stretching its head upward. The observation is of dubious value, since Geyr states that it took place at the top of a high and thick pine tree, he was not sure of the sexes involved, and could not see clearly! Brooks-King (1944) and Colyer (1944), in writing of the same species, describe a swaying from side to side of the male. Witherby *et al.* (1943) say that the chief feature of display is erection of the rump feathers. Sometimes the head is stretched up and the wings are fanned.

Gayner (1928) considered as courtship display of the song thrush an incident in which a male flew near and ran about a feeding female. The male tilted his head, gaped, puffed his breast, and expanded and depressed his tail feathers. The female made a *mock charge* and the pair flew off together.

Witherby *et al.* (*op. cit.*) say coition has been observed following this display, after which the female pecked into the open bill of the male (see Nero's observation, page 331). They further quote from A. Morley that sometimes the male displays by running at the female while in a semi-crouch, and then go on to say that W. Thompson has found this display to be associated with fighting as well as with mating behavior.

Regarding the mistle-thrush, Witherby *et al.* (*op. cit.*) say the chief feature of display seems to be flying pursuits from perch to perch, kept up for long periods of time. Such behavior was noted in robins on one occasion at Ho-Nee-Um. In this case (1947) a female was very persistently pursued through the branches of a tree by a male; the female eventually flew away and it could not be definitely determined whether the action indicated territorial defense, or was an unsuccessful attempt at mating. It could possibly have been both, with a female meeting an unreceptive male.

Witherby *et al.* also quote J. M. Boraston on the display of the ring-ouzel, *T. torquatus*. This is an unconvincing account of the male following the female, crouching, and flying at her, whereby she flew off. It sounds very much like typical robin combat.

No evidence was uncovered during the period of the study which would link the fighting between robins with any stage of pair-formation.

Table 1 summarizes the various types of display discussed in the literature (*re* the genus *Turdus*), showing the species for which they have been mentioned and indicating their status in relation to the robin.

Discounting the records quoted by Howell (*op. cit.*) of males feeding females on the nest, since presumably these were birds already long mated, it seems that the robin possibly possesses three of the display characteristics described for other thrushes: wing fanning, gaping, and chasing. None of these displays appear to be conspicuous in the robin, but their extent and variation remains to be determined.

THE PAIRING BOND

The robin generally remains constant to one mate for the entire nesting season. M11 and 9F remained together for three broods, both in 1947 and 1948. In the three years of the study, only two definite cases of mate-changing during the season were seen. In all other cases (16) where both members of a pair were banded, and remained on or near the area for successive nestings, the same mates were retained.

In 1948, 13F was mated for her first brood to a male designated as Mg (male-green) since he had lost part of his markings, but still retained a single green band. Both of

TABLE 1.—Reported patterns of mating display in the genus *Turdus*

Species	Head Stretch	Swaying	Wing Fanning	Gaping	Puffed Feathers	Courtship Feeding	Court. Chase
Blackbird	x	x	x	x	x	x	?
Song thrush	?	?	?	x	x	?	?
Mistle thrush	?	?	?	?	?	?	x
Ring ouzel	?	?	?	?	?	?	x
Robin	no?	no?	when copul.	?	no?	no?	?

these birds were gone for a period, but later in the year, 13F was seen feeding fledglings with M8. Shortly after this Mg was rediscovered alone, indicating that 13F had definitely changed mates.

The second case could be followed much more closely, and there was no question but that mates were clearly changed.

In 1949, 29F was mated to a male designated as Mu (male, unknown), since he had lost part of his markings, but could be recognized by green bands on each leg. He disappeared on May 1, probably through predation, while 29F was hatching a clutch. She remained with her nest, and by May 10 was joined by M12, who deserted his female, 30F, incubating a clutch in the adjoining territory. M12 adopted the territory vacated by Mu, along with 29F, and maintained it practically unchanged. The nest of 30F was destroyed on May 11, and she disappeared. The nest of 29F was also destroyed, but a short time later she started a new nest in the same territory, and the M12-29F mating persisted.

Nice (1930) also describes a case in which robins changed mates between broods.

Year to year constancy was not as predominant. The fact that robins tend to return to the same location each year enhances the chances of the same birds meeting during successive breeding seasons, but beyond this no definite tendency to pair again with last year's mate was noted. As previously mentioned, M11 and 9F were mated in 1947 and 1948, in the latter year after 9F routed a female which appeared to be paired with M11. However, in 1949 both were present but had new mates. M16 and 16F were mated in 1948, both were present in 1949, but also picked new mates. Nice (1944) observed the same pair of marked robins to remate three successive years. In this case the female also had to drive away another when she arrived late at the breeding grounds. Except for M11 and 9F, all robins observed at Ho-Nee-Um changed mates in successive years, one of the pair usually failing to appear at all.

For a few days in 1948, Mg vigorously defended the nest of his mate, 13F, and that of an unmarked female, who was also attended by an unmarked male. However, Mg soon restricted his interest to the nest of 13F. Other than this temporary activity, all behavior of the robins studied at Ho-Nee-Um indicated monogamous relationships. Examples of polygamy in this species have been described, however, in Howell (*op. cit.*).

DISCUSSION OF PAIRING BEHAVIOR

Such observations as are available indicate that courtship behavior in the Turdidae is not ostentatious, and suggest that it is not a highly evolved or complex behavioral pattern. In the case of the robin, no distinctive posturing, vocal activity, or behavioral modifications have been definitely assigned a pair-formation function.

Robins are ordinarily monogamous, and usually retain the same mate for the entire breeding season. If one mate is lost through death, or for some other reason, a new mate will be accepted. The re-matings which sometimes occur in successive years are probably due to chance.

THE NESTING ACTIVITY

The earliest nests were started during the first week of April in each year (see fig. 2). The time and stage of nest construction for each nest was deter-

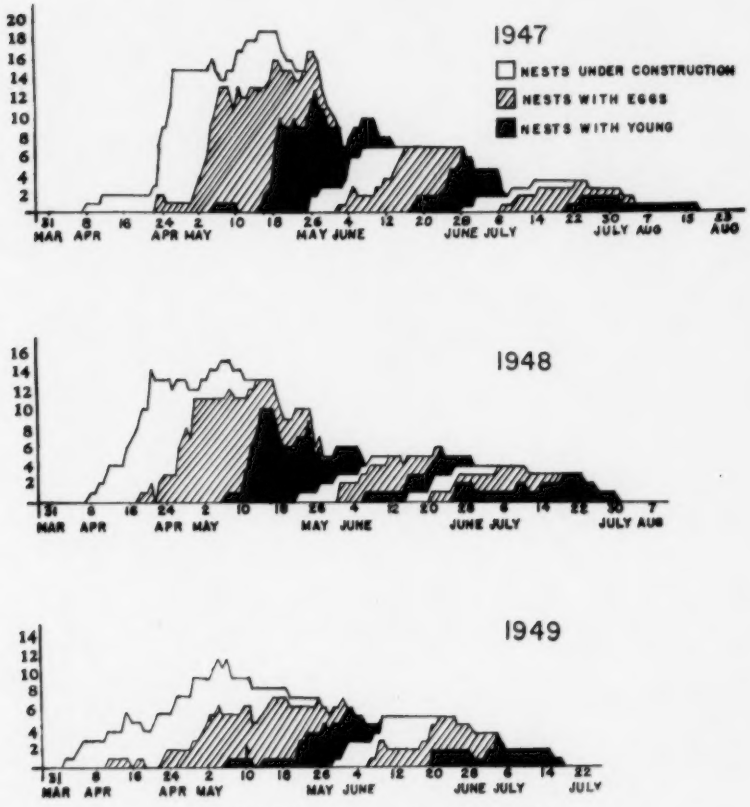
1947
NESTS UNDER CONSTRUCTION
NESTS WITH EGGS
NESTS WITH YOUNG
MAR APR APR MAY MAY JUNE JUNE JULY JULY AUG AUG
1948
MAR APR APR MAY MAY JUNE JUNE JULY JULY AUG
1949
MAR APR APR MAY MAY JUNE JUNE JULY JULY

Fig. 2.—Robin nesting cycles at Ho-Nee-Um

mined partly by daily visits and partly by interpolation. Four general steps in nest building were designated, and each nest found was assigned to one of the following categories: platform, half complete, nearly complete, and complete (lined but without eggs). Previously located nests in various stages of construction were followed, and averages determined for the length of time a nest would remain in a given condition. When a new nest was found, perhaps in an advanced stage of construction, it was thus possible to determine fairly accurately the date on which it was started. The period of nest construction varied from 3 (1 case) to 18 days (1 case), with an average of about 7 days (32 nest total). All information here and following (except nest elevation) refers only to *active* nests, those in which at least 1 egg was laid.

The Ho-Nee-Um area was of such size and nature that repeated searches insured the eventual discovery of practically 100% of the nests. It is believed that a majority of the nests at the cemetery was found, but no reasonable estimation of the population censused can be made. Other robin nests found in various convenient locations were studied as discovered.

NEST LOCATION

Despite the narrowness and open nature of the arbor vitae plantings at Ho-Nee-Um, the robins showed a definite preference for edge locations. Sixty out of 79 nestings in the plantings were peripherally located, and a tree directly at the edge was often chosen. The other Ho-Nee-Um nests were located outside of the main blocks of tree plantings. Edge effect could not be measured at the cemetery, since nesting cover was rather uniformly scattered over the area.

Nest height above the ground (202 nests) varied from 2 feet to 30 feet, with an average height of 7.4 feet (table 2). All of these figures are based on field estimates, and no actual measurements were made.

Preston (1946) found 7.4 feet to be the favorite nesting height for the robin, based on a study of 185 nests. The Madison data are from a biased sample, since tall trees were not thoroughly searched except at Ho-Nee-Um, and as a consequence, no nests were found at elevations higher than an estimated 30 feet.

Preston and Norris (1947) postulated that within a given species, the different individuals had favorite heights for nesting. However, Brackbill (1947) noted the sites of 3 consecutive nests of a particular female robin, and found no indication of her having a preference for a given nest height. Records at Ho-Nee-Um on nests of known birds gave the same general picture. For example, 9F built once at each of the following heights 3, 4, 5, 6, 7, 11′ and built 4 nests at 8′. In 1949, 34F built successive nests at the following heights: 8, 4, 7, 7, and 4′. Since all of these nests were in low trees, too great a variation cannot be expected. However, after building at 3 and 7. 4F (1949) next constructed a nest 19′ up in a box-elder, *Acer negundo*. Howell (*op. cit.*) found one nest 65′ above the ground. However, 50% of the 244 nests he checked were at heights of 10′ or lower, and half of the remainder were built at heights between 10 and 20′. Apparently 4 to 10′ is the usual height, with the selection inside this range probably due to chance location of a suitable nest site.

EGG LAYING AND INCUBATION

Egg laying started in April during each of the three years of the study. The earliest date for a first egg was April 12, the latest date for a first egg was July 22, and the latest date any nest contained eggs was August 5 (fig. 2).

Oviposition usually started about 3 or 4 days after the nest was completed. Not precisely measured, this varied from about 0 to 15 days, with no apparent reference to time of the season. In some cases the waiting period occurred

TABLE 2.—Number of robin nests found at different elevations

	Feet							
Year	0-4	5-8	9-12	13-15	16-19	20-23	24+	Total
1947	14	18	5	4	0	0	0	41
1948	25	40	16	2	3	1	2	89
1949	15	43	10	0	2	1	1	72
Total	54	101	31	6	5	2	3	202
Percent	27	50	15	3	3	1	1	100

TABLE 3.—Clutch size in robin nests*

Locality and year	Number of Eggs 1	2	3	4	5	6	Total	Aver.
**Ithaca '37	0	2	30	28	0	0	60	3.4
**Ithaca '38	1	3	35	27	1	0	67	3.4
Madison '47	0	1	14	15	0	0	30	3.5
Madison '48	0	2	27	41	0	0	70	3.6
Madison '49	1	0	30	14	1	0	46	3.3
Total	2	8	136	125	2	0	273	3.4 ± .05
Percent	1	3	50	46	1	—	100	—

* Omits obviously incomplete clutches.
** From Howell (1942).

TABLE 4.—Length of incubation*

Days	Number of Eggs Ith-aca**	Madi-son '47	Madi-son '48	Madi-son '49	Total	Per-cent
10	0	2	0	0	2	3
11	0	7	0	0	7	12
12	6	9	2	1	18	32
13	8	6	4	0	18	32
14	3	3	4	2	12	21
Total	17	27	10	3	57	100

* Based on marked eggs.
** From Howell (1942).
Average—12.5 days ± .14.

before the lining was put in the nest, the nest remaining for several days without any apparent work, after which a lining would be laid down, followed the next day by the first egg.

Eggs were ordinarily laid at the rate of 1 a day, although skipped days were common, and the clutch was usually 3 or 4 eggs. The average clutch was 3.4 ±.05 eggs (table 3). In cases where there were obvious signs of nest disturbance, such as a decrease in the number of eggs, or the presence of shells nearby, the nests were omitted from the computation of clutch averages. Some clutches as high as 8 eggs, which may represent the laying of two females, have been reported (Brooks 1933, Loveridge 1939). Howell (1942) mentions two robin nests which contained 7 eggs. In each case, however, it was definitely known that two females had laid in the same nest.

Sufficient data were not gathered on individual females to determine if some had a tendency towards larger clutches than others. Eight clutches from one female, 9F, are on record. In 1947 she laid 4 eggs in her 1st and 2nd clutches, 3 in her 3rd. In 1948 she laid 4 eggs in her 1st clutch, 3 in her 2nd and 3rd, and in 1949 she laid 3 eggs in her 1st clutch, 4 in her 2nd, did not lay a 3rd. Her average clutch, therefore, was 3.5 eggs. Four clutches are on record for 12F; each contained 3 eggs.

Incubation, defined as the time between clutch completion and hatching, averaged 12.5 ± .14 days (table 4). In the case of the 2 eggs with an apparent

10 day incubation period, it is probable that some incubation occurred before the clutch was completed. All incubation apparently was done by the females.

THE YOUNG

It was possible to make an accurate check of the time spent in the nest in the case of 56 young. The results of this study, compared with those of Howell (1942), are shown in table 5. The average time was 13.4 ±.13 days. The birds leaving the nest at the age of 10 days (Howell) were probably over-disturbed due to the fact that they were being weighed daily.

The earliest fledging recorded during this study was May 11 (1948). The latest was August 18 (1947). Fifty percent of all young (from 99 nests) fledged between May 21 and June 9, and 90% had fledged by July 20th.

Young robins usually left the nest before they could fly. This agrees with the observations of Howell (*op. cit.*), who found the largest number of young fledging on the thirteenth day after hatching, at an age when they could not maintain level flight.

All robin nestlings in the Ho-Nee-Um area were color-banded, but the heavy foliage, and the shyness of the birds, made it very difficult to trace the movements and activities of the fledglings. They called loudly and insistently, but immediately became quiet when they heard the alarm notes of the parents.

The first movements of the fledgling robins seem to be toward the nearest cover. They remain close to cover for about 10 days. After this stage they begin to move about more and do some food hunting of their own, although they usually do not become completely independent until about the 15th day after fledging, at which time they usually are 27 to 30 days old.

Most of the young were never seen again after fledging. Part of this disappearance was doubtless due to predation. In addition, field observations indicated that the young very quickly wandered from the original nesting territory, while still under parental care. Since the adults follow the young as they wander, this may be a factor in the abandonment of territories by many pairs.

The immatures seem to move quite widely after they have attained independence. There were 4 recoveries made out of 23 immatures (of unknown age) which wandered into the Ho-Nee-Um area from other places and were

TABLE 5.—Length of nestling period

Year and Locality	Days in Nest after Hatching								
	10	11	12	13	14	15	16	17	Total
*Ithaca '37	7**	2	3	5	4	0	0	0	21
*Ithaca '38	0	0	1	6	3	2	0	0	12
Madison '47	0	1	3	5	10	4	1	1	25
Madison '48	1**	0	0	3	5	6	0	0	15
Madison '49	0	0	0	4	7	5	0	0	16
Total	8**	3	7	23	29	17	1	1	89
Percent	9**	3	8	26	33	19	1	1	100

* From Howell (1942).

** Departure probably premature due to disturbance by observer. Average—13.4 ± .13 days.

trapped and color-marked there. In one case R. Nero saw a tail-marked young at the north end of the arboretum, just under one mile from Ho-Nee-Um, in a northeastern direction. The date and exact markings were not noted. J. Beer saw J3 (juvenile 3) about 1/4 mile north of the place of banding, 2 days after it had been marked. The writer saw J8, 4 days after marking, 1/4 mile south of the area, and J. T. Emlen saw J9 about 1 1/2 miles northwest of the area, 4 weeks after it had been banded. Furthermore, these birds may have wandered considerably prior to banding (table 6). None of them was ever seen again at Ho-Nee-Um.

Table 6 shows some maximum distances from the nests at which fledglings of known age were seen. Few records were obtained later than the 14th day after fledging. One young robin, however, was seen in the general vicinity of the study area on the 89th day after leaving the nest.

In the course of their wanderings, fledglings sometimes became separated from their parents, and were adopted by other adults. In 1947, M1 was seen feeding an unbanded fledgling, though all his own young were banded. In 1948 a fledgling of M11 was once seen being cared for by M13, and several times was seen in close association with M13's fledglings. Schantz (1939) describes a similar case.

All ties between parents and young are apparently broken when the latter become independent.

Flight ability is usually attained at an age of 14 or 15 days (Howell 1942). At this time the average fledgling has been out of the nest for 2 or 3 days.

Brackbill (1947) found young robins still partially dependent at 28 to 31 days of age; Howell (*op. cit.*) judges the period of dependency to be about 4 weeks. Independent fledglings were first noted in this study at an age of 29 days. Fledglings aged 20 and 25 days were trapped; in each case the parents remained nearby and made a great outcry when the traps were tended.

Females, at least sometimes, start the second clutch before the first brood is independent.

At Ho-Nee-Um, young robins of unknown age were observed in sexual behavior (see previous discussion), and in such social activities as fighting, chasing, and following. One was seen to sunbathe. Apparently while still learning to feed, one immature worried a chip of wood for several seconds; another unsuccessfully tried to eat a black swallow-tail butterfly, and was eventually scared away by the flapping of its wings.

TABLE 6.—Some maximum distances moved by fledgling robins

Days After Fledging	Yards From Nest
0*	50
1	75
2	80
3	130
10	175
14	425
28	1600
31	1800

* Day of fledging.

NESTING SUCCESS

Table 7 summarizes the nesting data gathered at Ho-Nee-Um and in the cemetery area. Only nests in which at least one egg was laid were recorded, and all nests which fledged at least one young were considered successful.

The table shows the nesting success of the robin in these area for the years studied. Additional data in the table show the degree of success attained in each year. The essential points in table 7 can be summarized as follows:

1. Success of robin nests studied varied from 32 (1949) to 62% (1948) with a three-year average of 49%.
2. Hatching success varied from 46 (1949) to 66% (1948) with a three-year average of 58%.
3. The percent of young fledged varied from 61 (1947) to 93 (1948) with a three-year average of 78.

Table 8 compares the nesting success of robins studied in these areas with nesting successes found in various other investigations. The average is considerably influenced by the large sample Kendeigh (1942) contributed. In some cases he did not check nests after the fledglings were fairly well developed, and *apparently successful* nests are included in his data. Omitting the Kendeigh

TABLE 7.—Robin nesting data

	No. Active Nests*	No. Successful**	% Successful	Number of Eggs	Av. Per Nest***	Number Hatched	% Hatched	No. of Fledglings	Average Per Successful Nest	% Young Fledged	% Eggs Producing Fledglings
Ho-Nee-Um '47	36	18	50	118	3.3	72	61	44	2.4	61	37
Ho-Nee-Um '48	26	16	62	83	3.6	55	66	41	2.7	75	49
Cemetery '48	53	30	57	173	3.4	109	63	101	3.4	93	58
Ho-Nee-Um '49	25	8	32	67	3.2	31	46	22	2.7	71	33
Cemetery '49	36	14	39	107	3.4	49	46	38	2.7	78	36
Total	176	86	49	548	3.4	316	58	246	2.9	78	45

* In which at least one egg was laid.
** Fledging at least one young.
*** Does not include obviously incomplete clutches.

TABLE 8.—Nesting successes of the robin

Number of Nests	Number Successful	Percent Successful	References
501	390	78	Kendeigh 1942
136	83	61	Howell 1942
64	49	77	Koehler 1945
16	2	13	Thomsen 1944
36	18*	50	This study 1947
79	46*	58	This study 1948
61	22*	36	This study 1949
893	610	68	Total

* Fledging at least one young.

sample gives an average of 60% successful, which is still well above the 49% success found at Ho-Nee-Um and the cemetery area (table 7).

Nice (1937), surveying the literature on open nests of passerines, found nest success varying from 39.5 to 53%, with an average (814 nests) of 45.9%. She found hatching success varying from 45.8 to 77.4% with an average (1994 eggs) of 61.4%. The fledging success in the studies she reviewed varied from 24.9 to 46.7%, with an average of 43% (1225 young). From this it would appear that the breeding success of the robin, as herein determined, agrees quite closely with that computed for the other open-nesting passerines, except that the survival of young robins from hatching to fledging time appears to be substantially higher than average.

In a previous paper (Young 1949a) the possibility of an inverse relationship between the hatching success and fledging success of passerines was suggested. The subject is of potential interest in relation to the studies of Lack (1947) and Errington (1946), but it should be pointed out at this time that the figures for the robin fail to show any correlation between the percent of eggs hatching and the percent of young fledging.

The percent of nests succeeding did not vary significantly from year to year, or between the areas studied. However, when each egg is taken as a reproductive attempt, and the percent of eggs producing fledglings is used as a measure of success, the robins nesting in the Forest Hills Cemetery during 1948 show a success which varies significantly from the average ($P < 1\%$), and were the most successful breeders of the groups here considered (table 7). Those nesting at Ho-Nee-Um in 1948 had a higher percentage of successful nests, apparently a slightly larger clutch on the average, and better hatching success. However, these factors were counterbalanced by a considerably higher mortality among the nestlings, so that in the actual production of young leaving the nest, they lagged behind the cemetery nesters. The ideal measurement of breeding success would be the production of young to independence, since the care of the fledged young should be considered as part of the reproductive attempt.

It was possible to record the total breeding activity of one bird, 9F, for the entire three-year period. During this time she made 10 known nesting attempts, of which 6 were successful. In her various efforts she hatched 21 out of 30 eggs (70%), and 16 (76%) of her young fledged. Such complete data were not available for any other individual female, but judging from data accumulated from all females, 9F's record was unusually successful.

There did not appear to be any relationship between population density and reproductive success. A drop of 28% in density at Ho-Nee-Um from 1947 to 1948 was associated with a 12% increase in successful nests, however in 1949, the year of lowest density (4% lower than 1948) there was a 30% drop in success (table 7). Furthermore, comparing those nests active during the periods of highest density (fig. 2) with other nests on the same area, failed to show any significant differences in success. Those nests active during the period of highest density in 1947 (May 16-19) were 62% successful, the others 40% successful, but the situation was reversed in 1948 when 55% of those active during the period of highest density (May 6-8) were successful, and the others were 67% successful. In 1949, nests active during the height of nesting (May 5-7) were 14% successful, others 39%, but combining the

three years, the success of 34 nests during the high density periods averages 50%, while 53 other nests average 47%. Errington (1945) found an inverse relationship between density and reproductive success in the northern bobwhite, *Colinus virginianus*, but Smith (1943) could not demonstrate it for the red-winged blackbird, *Agelaius phoeniceus*.

Comparison of nest successes according to elevations was handicapped by the lack of an adequate sample of nests from high elevations. One hundred sixty-two nests under 10′ in height were 49% successful, 32 nests over 10′ in height were 53% successful. Since these nests were gathered from all years (which had varying success) and from different areas (also varying in success), it is apparent that this slight difference cannot be considered significant. The most that can be said is that there is no apparent difference between the success of nests located at various elevations.

Other workers (Howell 1942, Stokes 1950), have found a higher percentage of nests successful in the late season than in the early part of the season. Only a slight tendency for this appears in the robin data (table 9). The differences are not statistically significant.

In many cases (at the Ho-Nee-Um area only) it was possible to estimate closely the time at which eggs or young disappeared from the nests. The data from this phase of the study have been used to plot the curve in fig 3. It may be noted that the total number of eggs, and the percent of young fledging, are not in complete agreement with similar data shown in table 7. This is due to the omission of nests in cases where the time of loss of eggs or young could not be closely estimated, and the inclusion of data gathered from nests on the periphery of the Ho-Nee-Um area, which were not included in table 7. The curves in fig 3 necessarily stop at the time of fledging, but in fig. 4 the data have been combined with those of Farner (1949) to form a life curve for the robin, dating from the time the egg first appears in the nest. It will be noted that the potential yearly increment to the population was halved before fledging. The curve in fig. 4 shows some positive skewness, which is not typical of vertebrate survival curves previously published (Deevey 1947). However, as Paynter (1949) has pointed out, when the accumulation of further data makes it possible to include very early mortality in other forms, more curves of this shape are to be expected.

Both survival curves (figs. 3, 4) contained an undetermined, but probably small, error due to the fact that some of the eggs lost were probably infertile.

TABLE 9.—Seasonal variation in robin nesting success*

Period	Total Nests	Successful	Failed	Percent Successful
Apr. 1-21	64	33	31	52
Apr. 22-May 12	67	39	28	58
May 13-Jun. 2	18	9	9	50
Jun. 3-23	15	10	5	67
Jun. 24-Jul. 14	9	6	3	67
Jul. 15-Aug. 3	----	----	----	----
Total	173	97	76	56

*Omits Ho-Nee-Um and cemetery nests for which the starting date could not be closely approximated, and includes nests from other Madison localities.

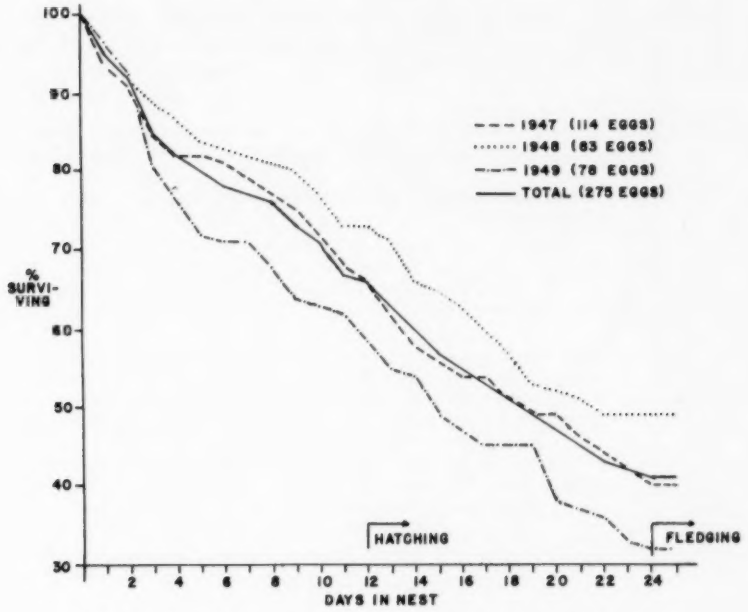

Fig. 3.—Egg and nesting survival of robins in the Ho-Nee-Um area

PERIOD OF RESIDENCE

Dates of abandonment of the breeding area do not necessarily indicate departures from the summer range, but may serve as a rough approximation, or may be used in computing minimum periods of residence. Approximate residence times for various individual robins are shown in table 10. The longest recorded period of residence for a male was 141 days and for a female it was 133 days.

TABLE 10.—Known periods of residence at breeding grounds

Bird	Sex	First Seen	Last Seen	Total Days of Residence
M1	M	Mar. 21 '48	Jul. 28	129
M11	M	Mar. 21 '48	Jul. 29	130
M14	M	Mar. 26 '48	Aug. 12	139
9F	F	Apr. 5 '48	Aug. 6	124
M9	M	Apr. 5 '48	Aug. 14	132
Mr	M	Mar. 21 '49	Aug. 9	141
24F	F	Mar. 26 '49	Jul. 5	101
16F	F	Mar. 29 '49	Jul. 13	106
M8	M	Mar. 29 '49	Jul. 20	113
wF	F	Apr. 2 '49	Aug. 13	133

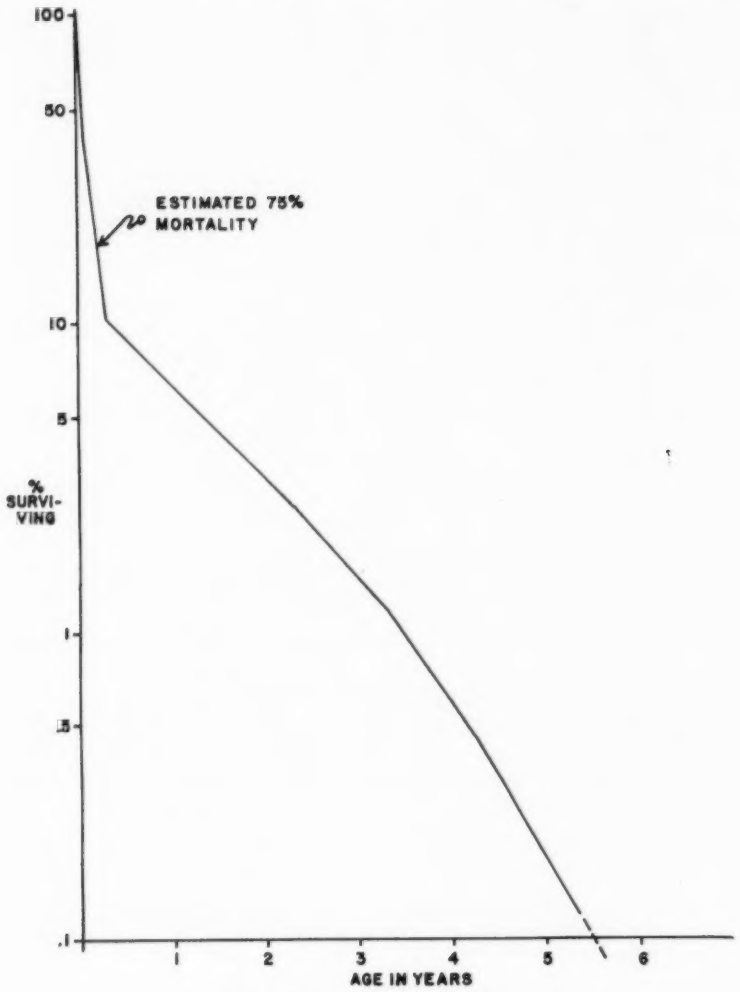

Fig. 4.—A life curve for the robin

THE NESTING SEASON AND POPULATION CHANGES

After an extensive survey of the literature, Howell (1942) concluded that all robins raise at least two broods every year. He then stated that few robins in the Ithaca, New York, region where he worked, raised three broods. Howell estimated that a maximum of 1 out of 7 pairs successfully raised three broods during a single breeding season. He did not mention any robins raising more than three broods. Ithaca is about the same latitude as Madison, and therefore has a summer breeding season of essentially equal length.

The following discussion is an attempt to correlate the careful work of Howell's (*op. cit.*) with certain field data gathered in the Madison region during this study, and with the valuable studies of Farner (1945, 1949) on longevity of the robin.

Field observations made during the spring and summer of 1947, 1948, and 1949 at Madison, Wisconsin, indicate the following:

1. Nesting starts about April 1, but the first big concentration of nests is not until the 3rd week of April (fig. 2).

2. One nesting cycle, plus care of the fledged young, takes about 40 days. (Data on 15 successful broods raised give an average of 39 days per brood, with a range from 33 to 47.) Howell gives examples (6 broods) ranging from 27 to 49 days, with an average of 39 days, and Howe (1898) lists 5 cycles varying from 30 to 45 days, with 37 days as the average.

3. Pairs whose nesting attempts failed started a new nest on an average of about 21 days after the start of the preceding attempt. This refers only to nests in which eggs were laid. Data on 75 failures give an average of 19.6 days expired between start of construction and destruction; data on 13 renestings after failure give an average of 1.2 days interval between the destruction and the start of the next nesting attempt.

4. Nest success (fledging of at least one young) in the Madison region averaged about 50% from April 1 through April 21 (64 nests), 56% from April 22 through June 2 (85 nests), 67% for later nests (24). See table 9. Howell (1942) found 47% success for *first nests* (96), and 82% for *second nests* (40).

5. Successful nesting attempts in the Madison region averaged about 3.0 fledglings (table 7). Howell (*op. cit.*) found an average of 2.4 fledglings each for 42 successful nests.

These field data have been used as the basis of a schematic diagram of the breeding season for the robin in the Madison region, in an attempt to simulate the changes in population size and composition. In order to construct the model it was also necessary to make the following assumptions, which are not supported by quantitative evidence, but seem reasonable in the light of general field observations:

1. The sex ratio is essentially 50:50.

2. There is no consequential non-breeding segment in the adult population arriving in spring.

3. Each pair will repeatedly nest again after failure, but can make no more than 5 nesting attempts.

4. Half of the robins stop breeding after the second successful brood, and all stop after the third.

Fig. 5 shows the distribution of nesting attempts by a hypothetical breeding population of 2000 robins (1000 pairs) under the conditions described above. It has been arranged to allow for the natural spread in arrival and start of nesting which might be expected, and an effort has been made to have the nesting attempts distributed in the manner indicated by field observations.

Mortality among adult robins is approximately 52% per annum (Farner 1949); assuming that this mortality is equal throughout the year gives an adult mortality of about 6% per month. Even in a species such as the robin, not subject to legal hunting, this mortality pattern could only be expected crudely to approximate the actual one. However, there is no information available that can be used to estimate a variable monthly mortality rate with any great

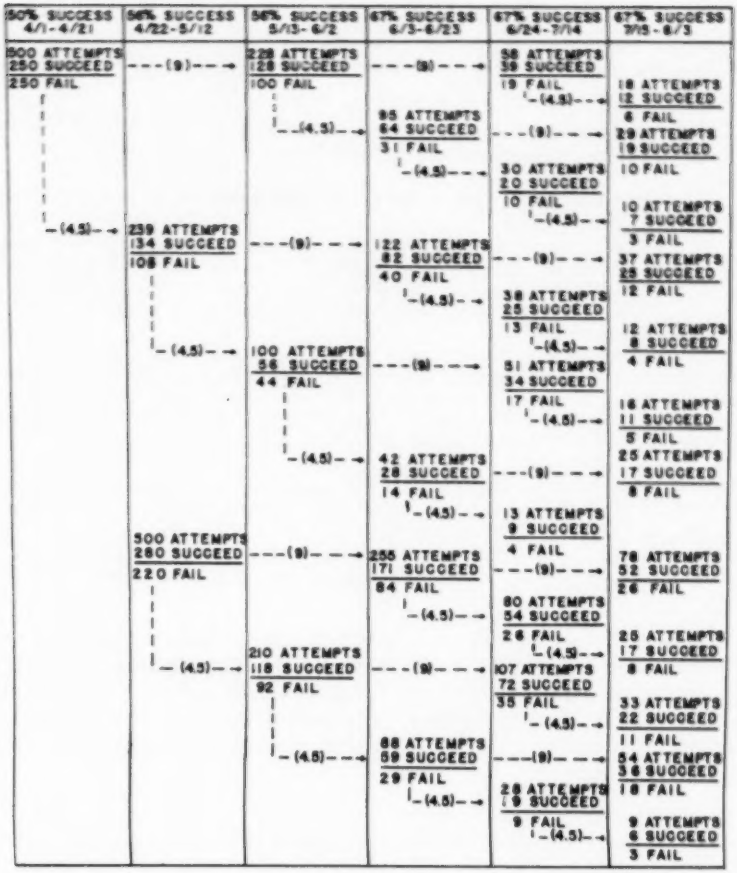

Fig. 5.—Schematic representation of the breeding activities of a hypothetical population of 2000 robins (figures in brackets state percentage of mortality among breeding adults).

degree of confidence. The mortality rate here used has been pro-rated for the different time periods shown in fig. 5, and is included in brackets on the arrows there. For example, of the 500 pairs attempting to nest in the April 1-21 period, half will succeed. Their first renesting will fall somewhere in the May 13-June 2 period, but during the intervening period they will suffer a 9% mortality.

On this basis, a hypothetical population of 1000 pairs arriving from late March to mid-April would make a total of 3130 nesting attempts (3.1 per pair) of which 1874 (60%) would be successful, as shown in fig. 5. Data on five groups of nests, totalling 174, and observed in the Madison region during 1947, 1948, and 1949 (table 7) give an average success of 49%, ranging from 32 to 62%. These nests, however, were mainly from the period before late

June, and the success ratio is possibly lowered for that reason. Howell (1942) found 55% success for the entire season, but the same objection applies to his data. It should be noted that Kendeigh (1942) reported 78% success for the robin, and the Koehlers (1945) reported 77% (table 8). Although these two estimates may be high, it would appear that 60% is not an unreasonable success for the entire season, and as a matter of fact this is the percent found when the data for table 8 is adjusted (see previous discussion under Nesting Success).

In the hypothetical population, 147 pairs (15%) would successfully raise 3 broods (Howell's estimate of 1 out of 7 equals 14%); 621 (62%) would successfully raise 2 broods; 191 (19%) would bring off a single brood, and only 41 pairs (4%) would fail to breed successfully. This would result in a total production of 5592 fledglings, averaging approximately 5.6 per season for each of the 1000 pairs which started the breeding period. Farner (1945) suggested that the average pair fledged somewhere around 5 young per season, which agrees surprisingly well with the present figure, considering the different methods of approach to the problem.

In computing mortality, Farner (*op. cit.*) chose November 1 as an initial date, but in a later paper (1949) made his calculations from January 1. The results do not differ greatly, and in this model young birds are considered to be essentially adult on November 1 as far as mortality pattern is considered. This reduces the period of time for which it is necessary to assign an arbitrary mortality rate. Farner (1945) estimated a 70% mortality between fledging and November 1, and computed that a total of 1400 young (for 1000 pairs) surviving to November 1 would be necessary to maintain a stable population. No data are as yet available for measuring early fledgling mortality, and Farner's estimate is here increased to 75% by the first November 1 in order to obtain the necessary residue of approximately 1400 young.

This does not imply that all young are subject to the same mortality rate (75%) whether they fledged from the first nesting attempt or last, but rather means that of all young fledged during the breeding season, only 25% survive to November 1. The actual mortality rates for the early periods after leaving the nest are unknown; table 11 is an example of an arbitrary mortality rate decreasing progressively with age. Applied to the figures on fledgling production in the hypothetical population (fig. 5) it gives the desired result.

Reduction of the 5592 fledglings by 75% gives a residue of 1398 at November 1. A mortality of 6% per month (52% per annum, Farner 1949) among adults reduces the 2000 arriving in spring to 1297 by the same date. The autumn age ratio in the model population then would be 1297 adults:1398 immature, or 93:100 as compared to Farner's 1945 calculation of 88:100.

Censuses taken in the Madison region during mid-August 1947, '48, and '49 (783 birds) gave a ratio of 166 adults:100 immatures. Both Farner's figures and the present calculations indicate that these census samples were strongly biased, since at this early date the excess of immatures would be expected to be even greater than on November 1 (see table 11). Partial separation of age groups was noted in the field, which may have been a contributing factor to the distortion, and there is a possibility of differential migration according to age, so that field censuses probably do not represent the true picture of age ratios in the area censused.

TABLE 11.—Seasonal changes in robin numbers as a result of breeding and mortality

Date	May 16			June 6			June 27			July 18			Aug 8			Aug 29			Sep 19			Oct 10			Oct 31	% Surviving	% Total pop.
Weeks until November 1	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0		
Number of young fledged and surviving	750	638	561	505	459	420	384	353	325	299	277	256	238	221	207	193	180	169	160	152	146	140	134	130	127	17	4.7
				1242	1056	929	836	761	696	637	586	539	496	459	425	395	367	343	320	299	281	261	254	244	234	19	8.7
							906	770	678	610	555	508	465	428	394	362	335	310	288	268	251	235	220	207	197	22	7.3
										1212	1030	906	815	742	679	621	571	525	483	447	413	384	357	334	312	26	11.6
													786	668	588	529	481	440	403	371	341	314	290	268	249	32	9.2
																696	592	521	469	427	391	358	329	303	279	40	10.3
Total fledged young alive	750	638	561	1747	1515	1349	2126	1884	1699	2758	2448	2209	2800	2518	2293	2796	2526	2308	2123	1964	1823	1698	1584	1486	1398	25	51.8
Adults surviving from April 1*	1825	1799	1774	1749	1727	1703	1679	1655	1632	1609	1586	1564	1542	1520	1499	1478	1457	1436	1416	1396	1376	1357	1338	1319	1297	65	48.2
Total adults and fledglings	2575	2437	2335	3496	3242	3052	3805	3539	3331	4367	4034	3773	4342	4038	3792	4274	3983	3744	3539	3360	3199	3055	2922	2805	2695	36	100.0
Adults per 100 immature	243	282	316	100	114	126	79	88	96	58	65	71	55	60	65	53	58	62	67	71	76	80	85	89	93	--	-----

*DX= 0.06 per month (0.014 per week)

Fledgling mortality

Age in weeks	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
DX	.150	.120	.100	.090	.085	.085	.080	.080	.080	.075	.075	.070	.070	.065	.065	.065	.060	.050	.050	.040	.040	.040	.030	.025	.015

Average age at fledging = 12 days

Average fledgling age at November 1 = 119 days

The graph of nesting activity (fig. 6) does not show close similarity between the hypothetical population described above and the data gathered from field observations. These discrepancies are due at least partly to bias in the field data. The major study areas contained large numbers of evergreen trees (*Thuja occidentalis, Picea* spp.) which were heavily utilized by the robins in the early part of the nesting season. Many birds left these areas after raising their first brood, and their subsequent breeding history was unknown. Howver, Howell (1942) has shown that deciduous trees are favored for later nestings, and it is probable that most of these birds bred again away from the study area. Also, nests are much more difficult to find in the tall, heavily foliaged deciduous trees than in the smaller shrub-like evergreens on the study areas. Though no new robin nests were found as late as July 15, one at Ho-Nee-Um (1947) was apparently started about July 14, and robins were several times seen carrying nesting material at even later dates. It is believed that a small number of robins do initiate new nesting activity in the latter half of July.

If the population remains stable, the fall cohort of 2695 robins in the model (1297 adults and 1398 young) must be reduced to 2000 by the following April 1. Considering all birds to be subject to adult mortality rates as of November 1 (according to table 11 the young would have an average age of 119 days), and assuming that adult mortality is not age-specific (Deevey 1947) the reduction can approximately be accomplished by applying again the 6% mortality per month (52% per year) which actually gives a spring population of 1978 birds.

It will be noted that in the preceding discussion an adult mortality rate (6% per month = .014 per week) is applied to birds 119 days of age, whereas in table 11, birds of the same age are subjected to a mortality rate of .065 per week, not attaining the adult mortality pattern until some 9 weeks later. The discrepancy reflects the shortcomings of the available data, and shows the gaps

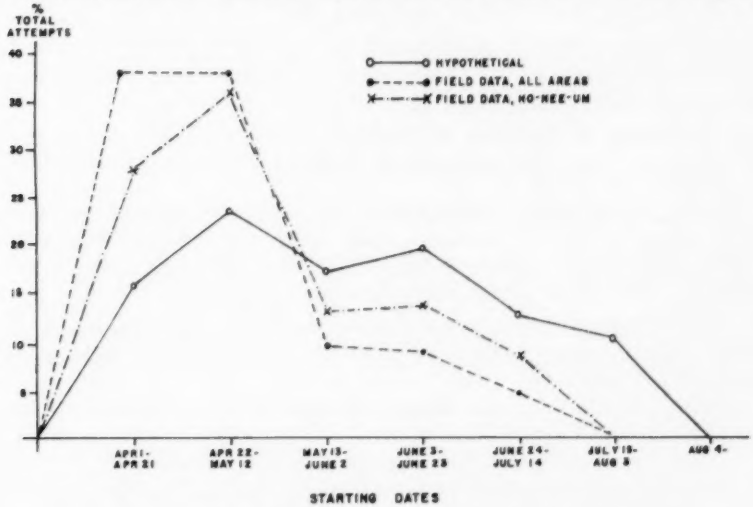

Fig. 6.—Hypothetical distribution of robin nesting attempts

in our knowledge for even such a common species as the robin. Since table 11 is used purely for illustrative purposes, and the model is not claimed as a perfect representation of robin population changes, further refinements in the treatment do not seem appropriate. The fact that enough data have been accumulated to make such a study possible at all is encouraging and may serve to stimulate further work in this important field.

SUMMARY

The breeding behavior and nesting activities of the robin were studied at Madison, Wisconsin, during the years 1947 to 1949, inclusive.

Pair formation in the robin apparently does not involve complex vocal, postural or behavioral modifications.

Robins are usually monogamous and pair for the breeding season. Rematings in successive years are probably due to chance.

Several examples of non-functional sexual activity were noted.

Nesting started in early April and extended to late July. Nest construction (32 nests) took from 3 (1 case) to 18 days (1 case) with an average of about 7 days.

Nest height (202 examples) varied from 2 to 30 feet with an average of 7.4 feet. Individual birds did not show any preference for a given height range. Nests in solid plantings were usually peripherally located.

The earliest date for a first egg was April 12; the latest date for a first egg was July 22. Oviposition usually started 3 or 4 days after the nest was completed.

Eggs were ordinarily laid at the rate of 1 a day; the average clutch was $3.4 \pm .05$ eggs. Incubation was done by the females; average duration was $12.5 \pm .14$ days.

The earliest fledging was on May 11, the latest on August 18. The average time spent in the nest after hatching was $13.4 \pm .13$ days, the young leaving before they could maintain level flight.

The young are dependent for about 2 weeks after they leave the nest. Fledglings wander widely; some become separated from their parents and are adopted by other adults.

Success of robin nests varied from 32 (1949) to 62% (1948) with a 3-year average of 49%. Hatching success varied from 46 (1949) to 66% (1948) with a 3-year average of 58%. The percent of young fledged varied from 61 (1947) to 93 (1948) with a three-year average of 78.

Considering each egg as a reproductive attempt, the robins nesting in the Forest Hills Cemetery (1948) were the most successful group, raising young from 58% of their eggs.

No relationship was found between nest success and nest density, nor between nest success and nest elevation.

A life curve for the robin, including egg mortality, is presented.

The longest period of residence on the breeding grounds was 141 days.

Analysis of hypothetical population, based as much as possible on field

data, suggests that a nesting success of about 60%, with an average annual production of 5 to 6 young per pair, associated with an approximately 75% mortality among young before autumn, and a 52% per annum mortality among adults, would result in a stable population.

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Origin of the North American Bird Fauna: Critique and Reinterpretation From the Standpoint of Continental Drift

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In attempting to trace the origin of any continental fauna one is faced inevitably with the problem of the nature of continents, for any postulations must be based on the past extent and relations of the continents and oceans. Current theories of the nature of continents may be titled briefly the concept of *permanence*, the concept of *drift*, and the concept of *land-bridges*. According to the proponents of permanence, the present continental masses and oceanic basins are regarded as relatively stable with their present spatial relations to each other and to the poles relatively unchanged since their origin or at least since the Paleozoic. According to the proponents of drift, the continental masses during the Mesozoic and Cenozoic were fundamentally different in extent, relation, and geographical position. The continents are believed to have originated as fragments of larger land masses and to have been displaced to their present positions. Both concepts agree that the relative amounts of land area and oceanic basin have not changed considerably, and hence, emphasize the *permanence* of the continents. In this regard, they differ from the concept of land-bridges which postulates loss of continents or extensive land bridges by foundering.

In a recent article, Mayr (1946) presents a stimulating and thorough analysis of the history of the North American avifauna, but all of his interpretations are based on the concept of permanence. The purpose of this paper is to discuss the interpretations based on permanence, and reëxamine the problem from the standpoint of continental drift using Mayr's data. I think it is possible to demonstrate that interpretations based on drift are just as plausible as those based on permanence and provide, in addition, an explanation for certain enigmatic problems posed by the assumption of permanence. Such a demonstration will not prove of course the occurrence of drift nor refute the concept of permanence or the concept of land bridges.

At this point it must be noted that some geologists are strongly opposed to the theory of continental drift. On the other hand, some geologists are strongly opposed to the concept of permanence. What must be recognized is *that the origin and history of the continents and ocean basins is not known* and that there is no more convincing evidence for permanence than there is for drift or land bridges. At present, all are theories to explain the origin of the present condition of the earth's crust (See Umbgrove 1947 and Nevin 1949 for a review and evaluation of the various concepts).

For an understanding of the analysis of the faunal elements a knowledge of Mayr's premises, methods, and conclusions, and the theory of continental drift are requisite. These are presented below and are followed by the analysis of the faunal elements.

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Mayr's Basic Premises, Methods, and Conclusions

Geological and climatic history of North America.—The following facts are regarded as fairly well established, although some points are controversial.

1. South America was separated from North America for the greater part of the Tertiary, probably from lower Eocene to upper Pliocene (see table 1 for geologic time scale). During that period, the region between Colombia and central Mexico was broken into a series of islands by several oceanic channels.
2. Asia and North America were repeatedly connected by dry land across Bering Strait during the Tertiary. This bridge is not regarded as being more extensive than the present shelf. It may have existed as recently as the last Ice Age.
3. The southern half of North America was tropical or subtropical in climate during most of the Tertiary.
4. The Bering Strait bridge has had arctic and subarctic conditions of day length from the Mesozoic to the present day. In the early Tertiary its climate was temperate. At present it is arctic and subarctic and passable primarily for birds of the tundra and coniferous forest.

TABLE 1.—Geologic time scale[1]

ERAS	PERIODS	EPOCHS	Rough estimate of duration in millions of years: EPOCHS	PERIODS	ERAS
Cenozoic	Quaternary	Recent	.025	1	75
		Pleistocene	1		
	Tertiary	Pliocene	11	74	
		Miocene	16		
		Oligocene	11		
		Eocene[2]	36		
Mesozoic	Cretaceous	Epochs not needed for present purposes		60	130
	Jurassic			30	
	Triassic			40	
Paleozoic	Periods and Epochs not needed for present purposes				300

[1] Modified from Simpson (1949, *The meaning of evolution.* Used with permission of the Yale University Press, New Haven).

[2] Includes the Paleocene which is older; its duration estimated at 17 million years.

Criteria for determination of place of origin.—Indirect methods are used almost entirely because of the absence of fossil data and consist essentially of a quantitative analysis of the distribution of the genera and species in a family. They are applicable and reliable, therefore, only in richly developed families. The region which shows the greatest differentiation is assumed to be the place of origin. In some cases the distribution of closely related forms is useful. Fossil data, which are the best criteria, are utilized whenever possible.

The faunal elements of the Americas.—Three Tertiary land masses have been the primary contributors to the present fauna of the Americas: *South America, North America,* and *Eurasia* or (*Old World*). The faunal elements from these land areas are recognized and named accordingly. There remains a large number of families and genera which cannot be readily placed. These groups are classified in the following faunal categories: *Unanalyzed, Panboreal, Pan-American,* and *Pantropical.*

The *Unanalyzed* category includes for the most part families that are widely and uniformly distributed. In some of these families, genera, and even species, occur in widely separated regions such as Africa, South America, and Australia. The *Panboreal* category includes groups with widespread, northern distribution that "have moved back and forth across Bering Strait so freely that they cannot be assigned with certainty to either continent." The *Pan-American* groups are so classified because they "crossed the Central American water gaps sufficiently freely to obscure their center of origin." The *Pantropical* element in the fauna is so similar in the Old World and New World tropics that the place of origin cannot be determined at present.

All of the families of birds in the Americas are classified on the basis of the seven categories described above. When possible the analysis is carried even further to subfamilies, genera, and species.

The Theory of Continental Drift

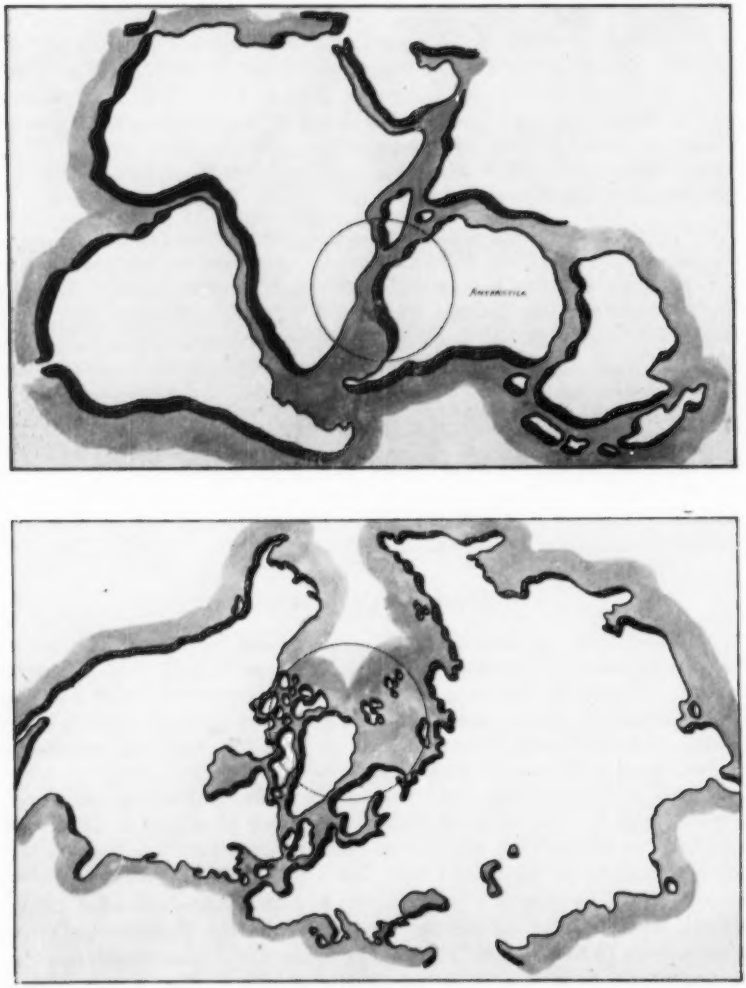
The theory of continental drift, or horizontal displacement of land masses, was first presented as a definite and defensible hypothesis by Taylor in 1908. He was followed by Baker in 1911, and Wegener in 1912 (see Du Toit 1937 for review). These early postulations differed much in numerous and fundamental details, but all were founded on large scale horizontal movements of land masses. Wegener's book was revised several times, and the fourth and latest German edition was published in 1928. A fifth edition was in preparation at the time of his death while exploring Greenland in 1930. New data for this edition were released in advance for a French edition (1937) which is available at the present time. Du Toit (1937) and Grabau (1940) have presented an extensive review of the problem, introduced some modifications, and presented further evidence for horizontal displacement. A revised edition (1953) of Du Toit's earlier study (1927) contributes new data bearing on the problem of a former land connection between South America and South Africa. The summary presented here is taken primarily from Du Toit.

1. Two great parent land masses, a northern one, *Laurasia,* and a southern one, *Gondwana,* were present throughout the Paleozoic and most of the Mesozoic.

These two major units were separated by a Mediterranean sea known as the Tethys.

Its trend was generally east-west; its depth varied, and several times its shallowing at some points put Gondwana into connection with Laurasia for short periods. By the Tertiary it was reduced considerably.

2. During the Cretaceous these parent masses fragmented, and the resultant parts began to drift apart. By the early Tertiary they had undergone marked changes in their spacing, orientation, shape, and relation to each other, but it was not until late Tertiary



Figs. 1-2.—1. (above) Gondwana during the Paleozoic and early Mesozoic (diagrammatic). The space between the various portions was then mostly land; 2. (below) Laurasia during the early Mesozoic (diagrammatic). The space between the various portions was partly land, partly sea. (Both redrawn freely from Du Toit. 1937. Based on Lambert's Equal Area Polar Projection.)

or Quaternary that the fragments reached approximately their present positions and relationships. The fragmentation and drift are regarded as still in progress.

3. With reference to the land masses as we know them today, from Gondwana the following evolved: South America, Africa, Arabia, Madagascar, peninsular India, Australia, and Antarctica.

From Laurasia evolved: North America, Greenland, Europe, and most of Asia.

The margins of the fragments at the time of fracture are not considered as identical with the present continental margins.

4. To indicate how the fragmentation occurred and the movements of the fragments attempts have been made to reassemble the parts.

The reassembly of the parts of Gondwana is illustrated in figure 1. It should be noted that the entire mass was located in the Southern Hemisphere and placed eccentrically with regard to the pole. The drift of the parts, with the exception of Antarctica, was dominantly northward. At the same time, however, there was apparently an eastward and westward drift, South America drifting westward relatively from Africa, and Africa and the other fragments drifting eastward. The actual direction of movement was probably radial.

The result of the fragmentation and drift of the parts was the creation of the *South Atlantic* and *Indian oceans*.

5. The reassembly of the fragments of Laurasia is shown in figure 2. The fragments were not as widely dispersed as those of Gondwana, but the same relative pattern of drift took place, namely, a northward, and an eastward and westward movement. North America moved ultimately northwestward, while Eurasia moved northeastward.

The result of fragmentation and drift was the creation of much of the *North Atlantic* and *Arctic oceans*. The southern part of the present North Atlantic was originally a small ocean (Poseidon), and it is supposed to have been the locus from which rifting started. Greenland may be considered as a point of reference from which North America drifted farther westward and Eurasia eastward.

After the Atlantic-Arctic rift appeared, North America and Asia still remained in contact and functioned probably as a bilobed mass joined by the narrow and relatively weak link made by Alaska and northeastern Siberia. With the displacement of Africa this double lobed mass was driven northwards over the pole from the European side before coming to rest in its present position. After reaching this northern position, North America and Eurasia continued their divergence and concomitant encroachment upon the basin of the Pacific. During the Mesozoic, therefore, and even earlier, Laurasia lay farther to the south, with much of its southern margin reaching or extending across the equator. Laurasia, then, has been displaced northward approximately 35° of latitude since Cretaceous time.

6. Laurasia and Gondwana are viewed as separate and in certain respects independent masses belonging to the Northern and Southern hemispheres. Although the fragments of both show the same drift pattern, their displacements have not been equal nor simultaneous. For example, in the early Cretaceous when Laurasia began to rift meridionally but showed no latitudinal drift, Gondwana had already fragmented and Africa (plus Arabia) drifting northward, came into *conflict* with Eurasia. The northward movement of Laurasia, by contrast, occurred primarily after the Mesozoic.

7. The rate of movement in drifting is assumed to be extremely slow at all times, usually rhythmic, but occasionally spasmodic.

Land Connections and Climatic Conditions

Since the present paper is concerned primarily with North America, below is a summary of its relations to other land masses according to the concept outlined above and the presumed climatic conditions of the connections according to Köppen and Wegener (1924).

1. North America was a part of a larger land mass (Laurasia) during most of the Mesozoic. The Atlantic rift which separated North America and Eurasia began in the southern-most portion in the Cretaceous and widened northward gradually during the Tertiary. Thus, there was a large intercontinental connection between North America and Eurasia for at least the first half of the Tertiary. The position of this connection in terms

of modern geography would be *across* the Arctic Ocean and the North Atlantic, as far south as the Iberian Peninsula on the European side and Nova Scotia on the American side, but displaced southwards about 35° of latitude.

2. Because Laurasia lay originally farther south, much of North America during the Cretaceous was tropical and subtropical, with the more northern portions (much of Canada and farther north) having a temperate climate. The connection between North America and Eurasia lay in tropical, subtropical, temperate, and arctic zones during the Mesozoic. As the rift moved northward and the continents drifted during the Tertiary, it was reduced to subtropical, temperate, and arctic zones, and finally to only temperate and arctic zones by late Tertiary.

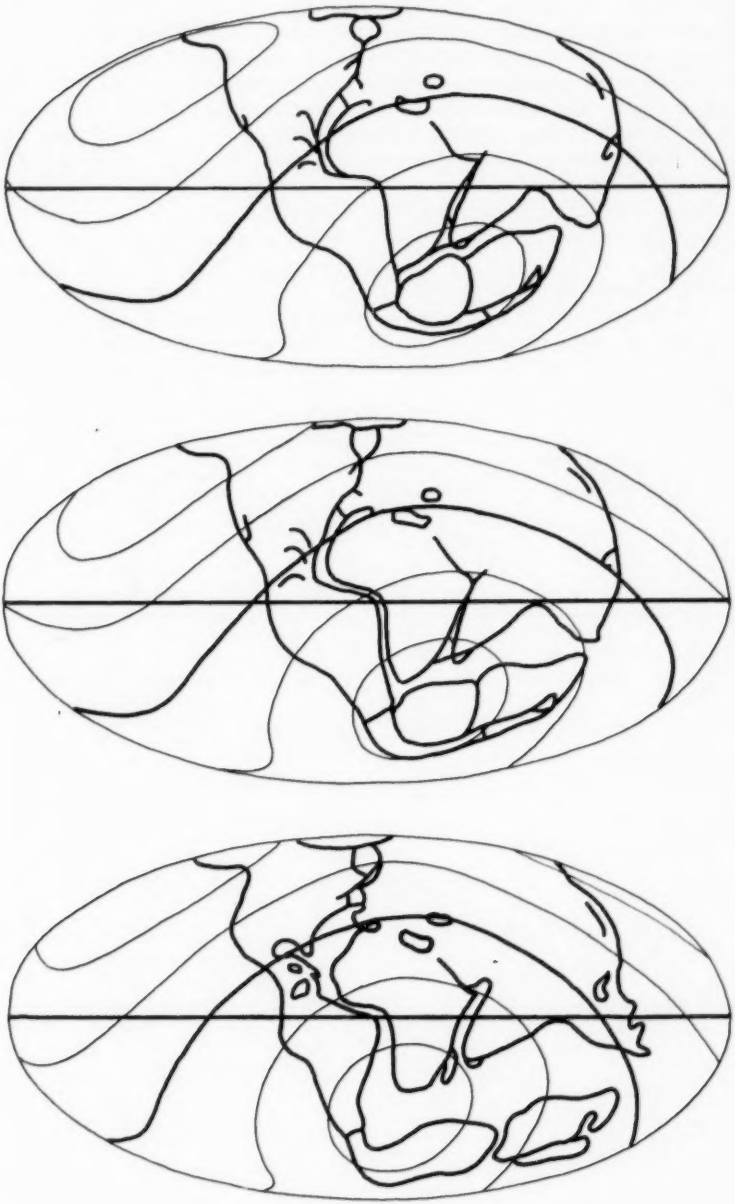
3. The connection became narrower as the rift widened and its only conspicuous vestige is the Bering Strait *bridge* which today straddles the Arctic Circle. Thus, what was earlier a broad *North Atlantic* connection with several climatic zones eventually became a North Pacific *bridge* in essentially one climatic zone.

4. Before the advent of drift (Cretaceous) North and South America were separated by the Tethys sea and portions of Central America. After drift began and until lower Eocene, direct land connections were possibly brought about irregularly through regressions of the Tethys or uplift. Island-chains were probably a constant feature of this region. In late Tertiary (upper Pliocene) North and South America achieved a direct land connection through Central America. During the Mesozoic and most of the Tertiary this region was in the tropical zone.

5. South America, as part of the southern land mass (Gondwana), was connected directly with what today is Africa and Antarctica. Indirectly it was connected to India and Australia. As Gondwana fragmented, South America lost its connection with Africa (by early Tertiary). The connection with Antarctica (and Australia indirectly) probably lasted through early or middle Tertiary. The connection with Africa in the Mesozoic lay in the tropical, subtropical, and temperate zones. The most southern portions of South America became warmer (from Arctic (?) to temperate) as it drifted northward. The major part of the continent has been in the tropical and temperate zones since the beginning of the Mesozoic, but these zones have been displaced northward and southward at various times.

Figures 3 through 7, which have been modified slightly from Köppen and Wegener (*op. cit.*), give a diagrammatic presentation of the climatic changes described above. In these figures the changing configuration of the land areas is based on Wegener's theory of continental drift, which is similar though not identical with that of Du Toit. Consequently, the movements shown may be disregarded. Only the regions within a climatic zone need be examined. It should be noted, also, that only the outlines of the continental areas are given. Shallow continental seas and major geosynclines have been omitted. In these figures the climatic zones are represented as shifting across the land masses which are drawn essentially in a fixed position in relation to the geographic poles and equator. It would be better to diagram the shifting of the land masses, but it has become customary to speak of polar *wanderings* or *migration* of the poles (and equator) and the diagrams are constructed from this point of view. It should be remembered, though, that the poles have not wandered or migrated. In the figures, the geographic equator is indicated on the horizontal axis of the elliptical outline; the climatic equator is indicated by the heavy line, and the zonation by the lighter lines which parallel the climatic equator.

That there have been marked climatic changes during geological history is an established fact. It also seems clear that there must have been climatic zones during all of geologic time if the inclination of the earth's axis has not changed markedly, as most astronomers and geophysicists maintain. The drifting of the land masses into lower or higher latitudes is one way of explaining

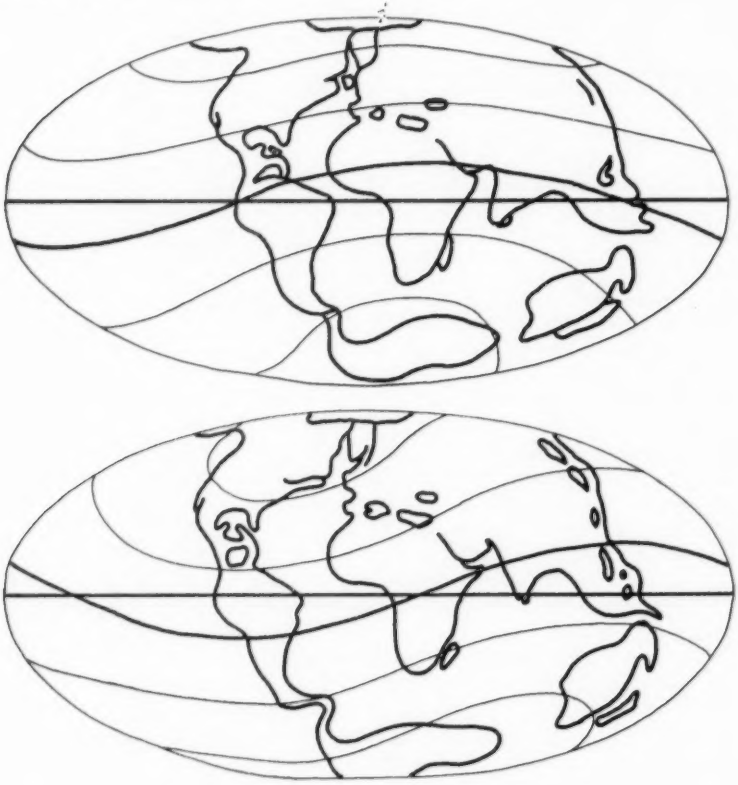


Figs. 3-5. Location of the equator (after Köppen and Wegener).—3. (above) Jurassic; 4. (center) Cretaceous; 5. (below) Eocene.

these climatic changes, but it is not the only way. It is also possible to explain them by means of geographic and astronomical factors (Brooks 1949), but it is interesting to note that some of the changes in geography which are postulated to account for climatic changes in the Upper Paleozoic do not differ much from the land connections postulated in the concept of drift (see for example, Brooks *op. cit.*, p. 248 and Umbgrove 1947, p. 282). It is obvious that neither theory alone provides an adequate explanation for all of the climatic changes, but irrespective of the explanation, the marked climatic changes of the geologic past have been established in broad outline.

Analysis of Faunal Elements

The purpose of this section is: 1) to present Mayr's data and interpretations for each of the faunal elements, 2) to comment on the interpretations and their implications, and 3) to present a reinterpretation of the data from the standpoint of continental drift.



Figs. 6, 7. Location of the equator (after Köppen and Wegener).—6. (above) Miocene; 7. (below) Pliocene.

THE UNANALYZED ELEMENT

Mayr's data and interpretations.—This element includes a large number of families of aquatic forms (marine, fresh water, or both) and a few families of strictly terrestrial species (table 2). In all of these families the distribution is world-wide or too uniform to postulate a center of origin. In a few cases indirect clues permit a guess for several of the terrestrial groups. The isolation of land masses, which is essential for the divergence of terrestrial faunas, has little bearing on the evolution of oceanic faunas.

What is most remarkable is that in many of these families it is not only the family that is widespread, but also the subfamilies, many of the genera, and frequently even the species and subspecies.

For the terrestrial families the evidence indicates that all of them originated at an early date, Eocene or Cretaceous (p. 15).

Commentary.—Since Mayr was primarily concerned with defining the place of origin of the various faunal elements one can understand readily why this group was not considered further than indicated above. However, this element is one of the largest in the American fauna and some discussion of its dispersal seems pertinent. Even if we have no clues at present for the determination of the place of origin, it is desirable to consider how these groups could have

TABLE 2.—Unanalyzed Element[1]

OCEANIC BIRDS	
Spheniscidae: penguins	Fregatidae: frigate-birds
Procellariiformes: tubinares	Phaëthontidae: tropic-birds
Chionidae: sheath-bills	Stercorariidae: skuas, jaegers
Sulidae: boobies, gannets	Laridae: gulls, terns
SHORE BIRDS	
Haematopodidae: oyster-catchers	Recurvirostridae: avocets, stilts
Charadriidae: plovers	Burhinidae: thick-knees
Scolopacidae: snipes, woodcocks, sandpipers	
FRESH-WATER BIRDS (partly marine)	
Colymbidae: grebes	Threskiornithidae: ibises
Pelecanidae: pelicans	Phoenicopteridae: flamingos
Phalacrocoracidae: cormorants	Anatidae: ducks, geese, swans
Ardeidae: herons	Rallidae: rails
Ciconiidae: storks	
LAND BIRDS	
Accipitridae: hawks, eagles	Apodidae: swifts
Pandionidae: osprey	N Picidae: woodpeckers
Falconidae: falcons, caracaras	O Hirundinidae: swallows
N[2] Caprimulgidae: nightjars	

[1] This table and all those that follow are from Mayr, 1946, pp. 26-27.

[2] N = probably originated in the New World. O = probably originated in the Old World. These symbols also apply in tables which follow.

become world-wide or uniformly distributed. Whether the place of origin was in the Old World or the New World, the problem still remains. (Truly oceanic birds are, of course, not included in the present discussion.)

A study of the literature reveals that groups with continuous or world-wide distributions have been neglected or abused in the formulation and analysis of biogeographic problems. Discontinuous distributions apparently (for example: South America, Africa, and Australia) have been regarded as more fruitful for study, especially in relation to the theories of drift and permanence, but it seems to me that a group with a world-wide or widespread distribution also presents a fundamental problem.

It is implied in current evolutionary theory that a group of animals stems from a single ancestral form which arose in a particular place at a particular time. Let us assume for the sake of argument that these places were widely divergent for many widespread, avian families, but not in North America, and that they arose in the late Mesozoic or early Tertiary. According to the proponents of permanence the two possible avenues of approach to North America during the Tertiary (and probably the late Mesozoic) were the Bering Strait *bridge* and the Central American *bridge*. It follows, therefore, that these families must have passed through the Bering bridge as they dispersed throughout the world, and not only the families as a whole but many genera as well. The only other alternative is to assume much transoceanic dispersal, which although credible for some cases, is hardly acceptable to account for the world-wide distribution of many forms.

Thus, a fundamental problem from the standpoint of permanence is: Could all of the widely distributed organisms have dispersed through the Bering Strait bridge? In analyzing this problem the following points are pertinent:

1. Bering Strait bridge probably never had a tropical or subtropical climate (Brooks 1949, Chaney 1940), yet many of the forms which are supposed to have dispersed through it are distinctly tropical. When we say *disperse through* it should be kept in mind that we mean gradual extension of range with periodic breeding cycles and not the mere movement across the bridge in one sweep from distant regions.

2. Practically the entire bridge has been subjected to arctic conditions of day length (assuming no marked change in the inclination of the earth's axis to the ecliptic). When one considers the importance of day length (photoperiod) in the flowering and physiology of plants and in the reproductive cycles and physiology of birds, it seems unlikely that these extreme day length conditions would have been conducive to the free dispersal of subtropical and even temperate faunas and floras. (Mayr raises this issue in his discussion of the dispersal of the Pantropical families.)

3. There is no evidence that the Bering bridge supported the ecological conditions demanded by the diverse organisms which presumably dispersed through it. Discussion of the dispersal of a genus or species tends to obscure the fact that in most cases it is not a single population of organisms that is dispersing but an aggregation of diverse organisms which are not only interdependent, but are adapted to certain conditions in the physical environment.

If we accept Bering bridge as the only bridge between the Old and New worlds since late Mesozoic, then strict adherence to the theory of permanence forces us to the view that we have had, for all practical purposes, a parade of the plant and animal kingdoms through it. When one considers the numerous, diverse groups of organisms with world-wide distribution, their differences in time of origin and mode of existence, the ecological concept of community

succession, and the importance of day length as a factor in reproduction and seasonal temperature conditions, one cannot help but question such a concept.

The preceding remarks have been made with regard to the distribution of organisms in general. If we consider now the avian families listed in the Unanalyzed Element and others with widespread distributions, we find many families that could have dispersed through the Bering bridge. The climatic and ecological conditions would have been no barrier to birds of the tundra, the high mountains, the northern coniferous forests, and the mixed forests, nor to many water birds, marsh birds, and land birds with wide climatic and ecologic tolerance. For the tropical and subtropical groups, however, the Bering bridge is not acceptable in the light of present knowledge of climatic conditions in the late Mesozoic and Cenozoic. (This question of the dispersal of tropical and subtropical forms is treated at greater length in the discussion of the Pantropical Element.) If one accepts the Bering bridge as the primary land bridge between the Old and New worlds, then not only the families in the Unanalyzed Element, but numerous families in other elements must have dispersed through it. Even granting considerable time and that these families probably did not appear there simultaneously, it seems to me that overmuch is being attributed to the Bering bridge.

Unanalyzed Element from the standpoint of drift.—According to the concept of drift, world-wide distributions are explained by the large, intercontinental connections and former proximity of the land masses. From any center of origin it is easy to conceive of dispersal throughout the land masses along latitudinal belts of similar climatic and day length conditions. The climatic and ecological difficulties posed by the concept of the Bering Strait bridge do not exist. What must follow though is that most of these groups are old groups, having originated by the end of the Eocene or even earlier. In this regard, Mayr's comment on the eight families of strictly terrestrial birds is relevant. He states (p. 15): "The evidence indicates that all of these families originated at such an early date (Eocene or Cretaceous) that subsequent shifts in distribution have obliterated most of the clues" (for determining the center of origin). Furthermore, when one examines the list of families in the Unanalyzed Element the large number of *older families* is striking. Without much fossil data the age of avian families cannot, of course, be dated accurately, but from the standpoint of structure and probable evolutionary sequence most of the families in this list are generally regarded as older families. Finally, the use of the Bering bridge at any time by those forms that were adapted to its prevailing climatic conditions is not precluded by the concept of drift. The Bering bridge may be viewed as the *northernmost* part of an originally much broader land connection in the region of the Arctic and North Atlantic oceans.

Conclusions.—The Bering Strait bridge could have been, and undoubtedly has been, used as an avenue of dispersal between the Old and New worlds. But when it is used as the only land bridge it would seem that too much is being attributed to it. When one considers the numerous organisms with world-wide or widespread distributions it seems improbable that all of them dispersed through the Bering bridge. From the standpoint of drift, widespread distributions, particularly in the older families, are not a difficult problem, and

the use of the Bering bridge at any time by those forms adapted to its ecological conditions is not precluded.

THE PANTROPICAL ELEMENT

Mayr's data and interpretations.—In the Unanalyzed Element families were found in various climatic zones, but there is a well-defined group of birds, and other vertebrates as well, that are widely distributed but confined to the tropics (fig. 8). This group includes five families of fresh-water birds (some partly marine) and three families of land birds (table 3). There can be no question of the faunal agreement between tropical-subtropical North America and the Old World. "It indicates that the present separation of the faunas is of comparatively recent date, and that it must have been preceded by a long period of faunal exchange" (Mayr, p. 34).

The area of origin is difficult to fix for each of the families of fresh water birds because there is little differentiation in either the Old or New World. All of them have widely disrupted ranges now, and Old World and New World populations often belong to the same species or superspecies. Among the families of land birds there has been much differentiation and both Old and New World tropics are rich in species. One the basis of present taxonomy and fossil data, the trogons probably originated in either tropical North America or the Oriental Region; the parrots, one of the richest of all bird families, probably originated in the Old World, but the great number of endemic genera and species in the Americas indicates a *very early* arrival in the New World. "This might well have taken place before the Eocene separation of South America from North America" (Mayr, p. 17).

Mayr concludes his analysis of this element by stating that these disrupted ranges of circumtropical families have "been used as *evidence* of former transatlantic or transpacific land connections by the advocates of such land bridges.

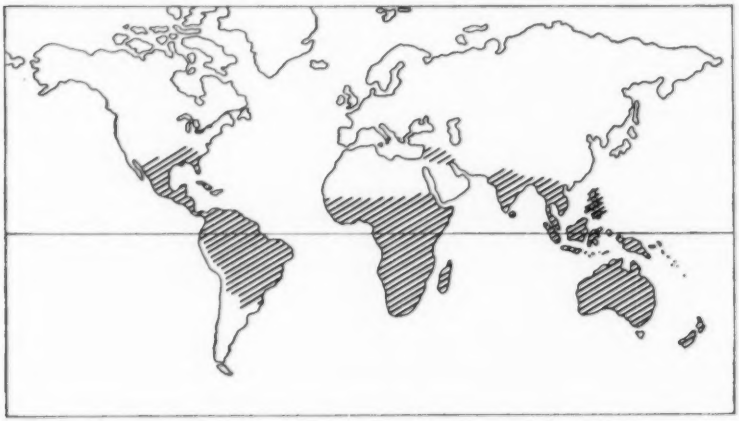


Fig. 8. Recent distribution of the anhingas (Anhingidae), one of the pantropical families. The family consists of one superspecies.

TABLE 3.—Pantropical Element

FRESH-WATER BIRDS (partly marine)	
Anhingidae: snake-birds	Rostratulidae: painted snipes
Heliornithidae: sun-grebes	Rhynchopidae: skimmers
Jacanidae: jacanas	
LAND BIRDS	
O Psittacidae: parrots	O Capitonidae: barbets
N Trogonidae: trogons	

We shall investigate in a later section how well founded their argument is." In the section on the problem of the Pantropical Element (pp. 34-37) Mayr reviews the problem objectively and does much to bring it into sharp focus. He does not state his own conclusions unequivocally, but it is apparent that he regards Bering Strait bridge as the pathway for the faunal exchange.

Commentary.—The early explanations for the pantropical distributions were conceived in the days when it was proper to erect land bridges wherever it seemed necessary to account for the observed distributions. As Mayr states, Matthew (1939) was instrumental in destroying many of these *bridges* because he showed that fossil records indicated that many pantropical families had much wider ranges (probably continuous across the Bering Strait bridge) in what are now the temperate zones. (Matthew considered the Bering Strait bridge as the only land bridge between the Old and New worlds.)

The primary basis of Matthew's thesis and those that follow him is that the explanation for present, disrupted, pantropical distribution lies in past *continuous* distributions. The proponents of this concept strive to point out, therefore, that disrupted disruptions were not present in the past *but are derived distributions.* They argue that there is no problem as long as one can show past continuous distributions; and they have striven to show that continuous distributions occurred in the past.

What has not been recognized apparently is that the problem not only still remains, but becomes a greater and more difficult one. Can we conceive of so many forms, tropical and temperate, extending their ranges gradually through Bering Strait, reaching the tropics eventually of either Old or New World, becoming extinct everywhere but in the tropics, and doing all of this without much evolution in form?

The problem of the passage of tropical forms through what was a temperate region climatically and an arctic one seasonally is recognized and elaborated by Mayr. He offers the suggestion that "perhaps the common ancestors of the tropical faunas in the Old and New worlds were not so narrowly tropical as are their living descendants" (p. 37). To illustrate, he points out that in the characteristically tropical family of trogons there are forms that live in the mountains where the climate is distinctly temperate. "Species with similar ecological requirements might have been able to exist in the warm temperate parts of Bering Strait bridge, even during the rather dark winter days." Yet, if that were true, might not one expect to find descendants of such stocks in north temperate latitudes today or in the late Tertiary? It is certainly possible that a tropical family or group may extend its range gradually and become adapted to temperate climates. In some groups that are primarily subtropical or tropi-

cal today, there are species or genera that occur outside of these regions (*e.g.* in the Psittacidae, Cuculidae, and Trochilidae). Furthermore, many present birds show wide climatic tolerance and it is also possible that present tropical distributions have been derived from ancestral stocks of this type. Either one of these explanations may be acceptable in a few cases, but it seems to me more likely that many groups which inhabit the tropics today did not exist for the most part outside of the tropical or subtropical (climatically speaking) regions in the past.

The possible use of the Bering Strait bridge in the dispersal of forest floras and mammals has recently been examined by Mason (1947) and Simpson (1947), respectively. Mason, in discussing the presumed migration of forest floras across Bering Strait writes (p. 206):

> "If we assume now that the poles have been stationary as most astronomers insist they have, and if we assume that the continents and ocean basins have been perpetuated in their present places through geological time as many geologists insist they have, we must conclude that no tropical, warm temperate, or even temperate forest flora, could possibly live and develop in high arctic latitudes. It would be too cold on the one hand, and too dark on the other hand. To raise the temperature in such an area and not change the long periods of darkness would only aggravate the situation because the increased temperatures would increase the respiration rate to the point that in evergreen species the reserve food supply would soon be depleted and deciduous species would be forced out of dormancy before adequate light returned and they too would dissipate their food reserves through rapid respiration. . . . Redwood forests just do not live in cold, dark, high polar latitudes; proof is needed that they ever did."

Simpson, when considering the question of the selectivity of the Bering Strait migration route, writes (p. 651):

> "In any event, and contrary to what seems to be a widespread impression . . . there is no evidence from the mammals that any truly tropical or subtropical animals ever migrated between Eurasia and North America [across Bering Strait], and it is even dubious whether any specifically warm temperate groups made this journey. The tapirs probably are the most nearly impressive evidence against this conclusion." Simpson presents evidence to show that the Bering bridge was the route of intermigration during the middle and late Cenozoic for Holarctic mammalian faunas, and that the migrants were generally "those groups tolerant of relatively cold climates." All of the faunal interchanges were selective and tended apparently to become more selective as time went on.

A possible solution to the problem of pantropical distributions would be: 1) a broad land connection in several climatic zones across the North Atlantic (Stegmann 1938); or 2) the assumption of a Laurasian continent as postulated by the theory of drift.

Mayr cites Stegmann (*op. cit.*) and Wulff (1943) as suggesting "a modified Wegenarian land connection across the North Atlantic lasting at least until the middle of the Tertiary" (p.36). He continues: "Simpson [1943, pp. 20-22], however, objects to this proposal on the basis of the small number of early Tertiary mammalian forms that were common to Europe and North America. A similar objection comes from the field of botany. The Eocene floras of Europe and North America 'were remarkably different' according to Reid and Chandler (1933, pp. 70-88). *There could have been no direct land connection between the two areas* [italics supplied]. Additional indirect evidence against a transatlantic bridge is provided by the fact that the American fauna is much closer to the southeast Asiatic than to the European-African fauna."

It is beyond the scope of the present paper to evaluate all of the mammalian and botanical evidence for the existence of a North Atlantic land bridge. But in view of the strong position taken by Mayr, and the fact that the Bering bridge was probably not suitable for the passage of tropical and subtropical forms, these objections must be scrutinized. This issue is an important one, for a broad land connection across the North Atlantic in several climatic zones would provide an explanation for a number of biogeographic problems irrespective of the concept of continental drift.

There can be no doubt that Mayr's statement of Simpson's objection is in error. The fact is: There is an "unusually close similarity of early Eocene faunas in Europe and North America" (Simpson 1947, p. 658). Simpson does, however, object to a North Atlantic connection. The basis of his position is evident in the following quotations (Simpson 1947, p. 658, italics supplied):

1) ". . . It is fairly clear that the tendency has been to stress the Atlantic route for the early Tertiary and the Pacific route thereafter. *That the early Cenozoic connection of North America was with Europe* and that this was replaced, or first supplemented and then replaced sometime during the Tertiary by a connection with Asia has become almost an article of faith to the supporters of continental drift, but they did not originate this idea, and *it is probably now the majority opinion even among the opponents of continental drift.*" 2) "About the only concrete evidence for an early Tertiary Atlantic bridge or corridor is the *unusually close similarity of early Eocene faunas in Europe and North America.*" 3) "Close as was the early Eocene faunal relationship between western Europe and North America, it was little if any closer than for the Recent mammalian faunas of the same areas. This does not rule out an Atlantic bridge, but it shows that a Bering bridge could adequately account for all of the facts. The Recent resemblance is almost certainly due to a Bering bridge only."

It would seem from Simpson's statements that the *present facts* point to a North Atlantic connection in the early Tertiary, and a Bering Strait connection in the late Tertiary and Quaternary. Simpson's objection to the North Atlantic connection rests solely, at present, on a matter of interpretation.

"The needed direct evidence is knowledge of the early Eocene mammals of Asia, and especially of northeastern Asia. A few probably early Eocene forms have been found in Asia . . . but so very few that they show only that some relationship with both Europe and America did exist *without really casting any light on the relative degree of relationship* or, secondarily, *the position of the bridge or bridges responsible for this.* The only known Asiatic Paleocene fauna . . . is of such peculiar facies that it certainly does not represent the source of the early Eocene migrants and casts little light on Paleocene continental relationships. It does suggest closer relationships with America than with Europe, *but the evidence is quite insufficient* for any reliance on this hint" (Simpson 1947, p. 658, italics supplied).

It seems also that Mayr's statement, that the Eocene floras of Europe and North America "were remarkably different" according to Reid and Chandler, is in error. Reid and Chandler concluded (1933, p. 88) that "it does not appear possible to make a close comparison between the Eocene flora of America and that of the London clay" (Lower Eocene). To understand why Reid and Chandler could not have reached the conclusion attributed to them and to explain the source of the quotation cited by Mayr, one must examine the context.

In Part VII of the Introduction (pp. 82-89) Reid and Chandler discuss the relation of the London Clay flora to other Eocene floras of similar age.

They point out early in their discussion of the European Eocene floras that "it is extremely difficult to compare the London Clay flora with other fossil floras for more than one reason. In the first place, with the exception of a few species in a few deposits, all European Eocene floras have been determined from *leaves*, whereas the London Clay flora has been determined from *fruits and seeds*" (p. 82, italics supplied). We pass over their comparison with the European floras and come next to the American Eocene floras, the discussion of which is pertinent. They state: "Like the European Eocene floras, nearly all those of America have been determined from leaves. It will be readily understood therefore that the terms of comparison are even fewer than in the case of the European floras, and that no useful purpose can be served by attempting such a comparison" (p. 87). Nevertheless, they do discuss one flora, the Brandon Lignite of Vermont, which is represented by a wide range of plant parts, including some fruits, seeds, and wood. The most startling fact about this flora is that there is no stratigraphical or direct evidence to show its age. It is underlaid by Cambrian and overlaid by Quaternary. Since only a small portion of the fossils could be placed in modern genera (Perkins 1904, 1906), Reid and Chandler "think it probable that the Brandon Lignite must definitely be older than Miocene." (Berry (1919) stated his opinion that it was possibly Oligocene, but that it is probably Eocene. In a letter to Reid and Chandler (March 5, 1930) he wrote "that there be scarcely a doubt but that the Brandon is Eocene.") In conclusion, Reid and Chandler state (p. 88):

> "There may be some relationship of what degree we can form no opinion, between two or three of the genera found in the London Clay and Brandon Lignite, but the illustrations (Perkins, *op. cit.*) make it clear that the species are remarkably different. Especially do they differ in the much greater size of the Brandon fruits. We do not think they offer any valuable grounds for correlation. Thus it does not appear possible to make a close comparison between the Eocene flora of America and that of the London Clay."

Recent studies of the Brandon Lignite and a restatement of the problem by Barghoorn and Spackman (1949) corroborate Reid and Chandler's conclusion. On the question of the age of the Brandon flora, which is of primary importance, Barghoorn and Spackman make the following statements:

> 1) There is no direct method available for dating the deposit. 2) It would seem logical to regard it as early or mid-Tertiary in age on the basis of paleoecological evidence. 3) The possible early or middle Tertiary age is somewhat inconsistent with its present physiographic relationships, which place the age of the deposit as Pliocene, or at most late Miocene. The deposit, and its associated clays, ochres, and ores, cannot be referred to the early Tertiary without necessitating a thorough reinterpretation of the Cenozoic erosional history of western New England. 4) There is no critical botanical evidence to establish the Eocene age of the Brandon flora as proposed by Berry (1919) and others. 5) The problem of the age of the Brandon Lignite cannot be resolved until more is known of its geological relations and its possible paleobotanical correlation.

Barghoorn and Spackman do not compare the Brandon flora with other floras in this preliminary report, but they do mention the London Clay flora when they discuss the family Nyssaceae,

> "one of the most interesting and significant groups represented in the Brandon Lignite. As the result of histological studies a particularly striking series of fruits designated by Perkins (*op. cit*) as *Monocarpellites, Bicarpellites, Tricarpellites,* and *Glossocarpellites* have proved to be endocarps of Nyssaceous fruits. Several of the two and three carpellate forms are comparable to the London Clay fruits *Protonyssa* and *Paleonyssa* described by Reid and Chandler (1933)."

With regard to Eocene floras in general, Good, in his recent treatise on the geography of flowering plants, states (1947, pp. 246-247):

> 1) The Eocene floras were much like those of the Cretaceous. 2) "There was no appreciable break between the two periods either in plants or in climate, and the latter was, so far as vegetation is concerned, apparently an extension of the former." 3) "The two together suggest strongly that there may have been something in the nature of a single extensive and generalized flora over much of the whole world or at least the Northern Hemisphere."

Mayr's final objection to the North Atlantic connection, the fact that the present American fauna is much closer to the present southeast Asiatic than to the European-African, rests on a matter of interpretation. As Mayr pointed out, this is indirect evidence. Though there is some affinity between the present American fauna and the present southeast Asiatic fauna, I cannot see that it necessarily follows that this supports the concept of a Bering Strait bridge and opposes a North Atlantic one. The present distribution can also be explained in part by dispersal in the past through similar climatic or ecological zones, and then survival in those areas which changed the least ecologically since the late Mesozoic. For example, the present Indo-Malaysian flora contains about 70% of the genera or closely allied genera known from the London Clay flora. On these grounds, Reid and Chandler concluded that the London Clay flora reached England by migrating from the Indo-Malaysian region along the Tethys Sea. If the flora was widespread in the tropics and subtropics of the Eocene, as seems probable from Good's conclusions and Reid and Chandler's data, then the fact that the greatest number of these Eocene genera are found living today in the Indo-Malaysian region does not necessarily indicate that the flora originated in that region. What it seems to me to indicate is *that an old, widespread, tropical, or subtropical flora has survived to the greatest extent in a region which has changed relatively little climatically from the Eocene to the present day.* This interpretation may be applicable also in many other families of organisms in which the highest concentration of species or genera is found in the Indo-Malaysian region. Other tropical regions which have apparently experienced relatively little change since the Eocene with respect to the climatic equator are Central America, northern South America, and parts of Australia.

On the basis of the mammalian and botanical paleontological evidence presented above it is apparent that the known biogeographic data are not at variance with the concept of a North Atlantic connection. But what is most important is that on the basis of recent geological studies Eardley (1948) concluded that the crust of the North Atlantic and Greenland Sea underwent movements in Tertiary time sufficient to provide land bridges between Europe and North America, possibly on several occasions. Eardley also concluded that the Alaska-northeastern Siberia region was one of nearly constant land connection during the Mesozoic and Cenozoic and probably also during the Paleozoic. In neither case, unfortunately, is information available with respect to the southern limit of these land connections.

Pantropical Element from the standpoint of drift.—At the beginning of the previous discussion it was pointed out that either a broad North Atlantic land

connection or a Laurasian continent as postulated by the theory of drift could explain pantropical distributions. If a North Atlantic bridge did exist, and if such a bridge could explain pantropical distributions, then the existence of a Laurasian continent and its subsequent fragmentation and drift could also explain them. The concept of drift provides an explanation for a broad North Atlantic connection, but such a connection might be possible, of course, without postulating drift.

From the standpoint of drift as a whole, present pantropical distributions may be explained as follows. When the continental masses lay farther to the south much of their area was tropical and subtropical. There developed at this time a tropical avifauna of wide distribution in Gondwana and Laurasia embracing what are now separate continents. As the land masses drifted northward, the climatic conditions changed gradually causing the extinction and/or retreat of the tropical and subtropical faunas from higher latitudes. Concomitant with the northward drift there was fragmentation of Laurasia and Gondwana. The result is the present restriction of the older, widespread tropical fauna to the present tropical zone with discontinuous distribution of surviving groups.

Conclusions.—To explain the distribution of the pantropical groups from the standpoint of permanence would seem to require:

1) the assumption of a tropical center of origin; 2) the acceptance of Bering bridge as the sole avenue of faunal exchange; 3) the movement of forms in both directions across it unless we assume that all of the pantropical forms originated in either the Old or New World; 4) the assumption that some aspects of the physiology of these forms, or their ancestors, were sufficiently different to permit them to extend their range through temperate regions as regards temperature and arctic and subarctic regions as regards day length; 5) the assumption that this extension of range into higher latitudes and significantly different environmental conditions did not produce new genera, (not even distinctly different species in a few cases); and finally, 6) the assumption that these extensive populations of adapted forms became completely extinct over the entire route of migration surviving only in the tropics today.

According to the drift theory and assuming a similar tropical origin, the explanation of the present distribution of pantropical groups requires:

1) the assumption of a more or less continuous tropical fauna restricted to the tropical zone of Laurasia and Gondwana; 2) the fragmentation and drift of the original land masses to produce the present continental masses; 3) the concomitant isolation of segments of the original fauna resulting in present discontinuous distributions; and 4) the survival of some of the original tropical groups in the present tropical zone, with further evolution or extinction in these groups in parts of that zone.

From the above summary, it is evident that pantropical distributions *can* be explained by the theory of permanence or by the theory of drift. If one considers the probability of each explanation as a whole in the light of present knowledge, it is difficult to defend a preference for either one. But if one accepts the concepts of permanence and drift as assumptions of equal probability, then the explanation based on drift would seem to me to be the more probable.

THE PANBOREAL ELEMENT

Mayr's data and interpretations.—There is a group of circumboreal birds, of which the loons, the phalaropes, and the auk family are typical (table 4).

TABLE 4.—Panboreal Element

Gaviidae: loons	Phalaropodidae, phalaropes (and
Alcidae: auks, murres, puffins	many other groups of shore birds)

All three families are distributed in the arctic or north temperate zone and are well represented in the Old and New worlds. Furthermore, more than 80 per cent of the tundra zone *species* of these groups and others are circumboreal. These facts make it impossible to determine the original source for these families.

This close resemblance between Eurasia and America is explained by Mayr by the existence of the Bering bridge for "a good part of the Tertiary."

Commentary.—In the light of present knowledge, a Bering bridge would not have been a barrier to the free dispersal of boreal and arctic forms; and when one considers the habits of some of these forms it is unlikely that a land bridge is necessary to explain their distribution.

Panboreal Element from the standpoint of continental drift.—From the standpoint of drift the Panboreal Element is explained by the continuity of Laurasia during most of the Tertiary and the failure of its fragments to become completely isolated. Bering bridge, as described earlier, represents the remaining *connection* between North America and Eurasia and has been in existence since the origin of Laurasia.

Conclusions.—The distribution of the Panboreal Element can be explained readily by either the concept of drift or permanence.

THE OLD WORLD ELEMENT

Mayr's data and interpretations.—The connection between Asia and North America across Bering Strait is ancient (pre-Tertiary). A more or less active faunal exchange probably took place through the Tertiary even when water separated the two continents. "This long-standing accessibility of North America to Old World immigrants is reflected in the taxonomic composition of the Old World Element in America." Depending on their time of arrival, these birds have either 1) not changed at all; 2) become subspecifically distinct; or 3) evolved into separate species, genera, or subfamilies if they arrived early.

Birds that have not changed at all include the Alaska Yellow Wagtail (*Motacilla flava alascensis*), the Red-spotted Bluethroat (*Luscinia suecica robusta*), and the Wheatear (*O. o. oenanthe*). Species that have become subspecifically distinct include Kennicott's Willow Warbler (*Phylloscopus borealis kennicotti*), the Northern Shrike (*Lanius excubitor borealis*), and the Brown Creeper (*Certhia familiaris americana*). The last category, those birds that arrived early and evolved into separate genera or species, or even subfamilies, contains a large number of diverse groups. In the case of the Strigidae, the invasion was very early since there are now six endemic genera in the New World, and four fossil species of the extinct family Protostrigidae are known from the Eocene of North America (Wetmore 1940). The families in this Element (table 5) are classified according to their time of arrival, the basis being the amount of differentiation in the Americas.

TABLE 5.—Old World Element

EARLY IMMIGRANTS	
Gruidae: cranes	Strigidae: typical owls
Columbidae: pigeons	Corvidae: crows, jays (part)
Cuculidae: cuckoos	Turdinae: thrushes (part)
FAIRLY EARLY	
Alcedinidae: kingfishers	"Chamaeidae": wren-tit
Corvidae: crows, jays (part)	Motacillidae: wagtails, pipits
Paridae: titmice	Carduelinae: cardueline finches (part)
Sittidae: nuthatches	
RECENT	
Tytonidae: barn owls	Turdinae: thrushes (part)
Alaudidae: larks	Sylviinae: Old World warblers, kinglets
Hirundinidae: swallows (part)	Laniidae: shrikes
Certhiidae: creepers	Carduelinae: cardueline finches (part)

[Also of Old World origin are the Phasianidae, represented in the Americas by the quail (subfamily Odontophorinae); and the Muscicapidae, to which the American subfamily gnatcatchers (Polioptilinae) is undoubtedly related.]

Commentary.—The Old World origin of a number of the families listed seems beyond question. In other cases, as Mayr points out, the evidence is inadequate for any convincing conclusion. However, whether a group originated in North America or the Old World the problem is still the same, to account for its present distribution, and according to the theory of permanence that means the use of Bering bridge solely.

For the recent immigrants from the Old World, dispersal through the Bering bridge is evident. All of these forms have a wide climatic tolerance or are essentially temperate or boreal forms (*e.g. Tyto alba, Eremophila alpestris, Hirundo rustica, R. riparia, Certhia familiaris*). Moreover, those forms, cited earlier, which have recently entered Alaska from Asia and are not subspecifically distinct, demonstrate clearly that there is dispersal across Bering Strait when the ecological requirements of the species are met. For the early and fairly early immigrants, however, it is questionable whether the Bering bridge would have been suitable for all of them. Although a number of these groups have some temperate forms, it seems possible that they originated in the tropics or low latitudes and that the temperate forms are a more recent adaptation. If a tropical origin could be established for these groups, their use of the Bering bridge as an avenue of dispersal would be less probable. Judging from their present distribution and the fact that some of them show secondary centers of evolution in the tropics and subtropics of the New World, the following groups may well have had a tropical or subtropical origin: Columbidae, Cuculidae, Turdinae (in part), Corvidae (in part), Alcedinidae. However, it is not possible at present to rule out completely the possibility that a group could have arisen and become well developed in the tropics of the Old World, dispersed by means of a few forms through the temperate zone into the New World, dispersed toward the tropics in the New World and here have developed a secondary center of evolution.

Old World Element according to drift.—From the standpoint of drift the distribution of the early and fairly early immigrants is explained by the land connections between, or the proximity of, the present continents during the Eocene. The avenues of dispersal would have been in tropical, subtropical, and temperate regions and would have permitted the free dispersal of the forms under discussion, or of the ancestral stocks. The dispersal of the recent immigrants can be explained by the continuous availability of a bridge between Eurasia and North America throughout Cenozoic time, but as Laurasia drifted northward the bridge would have become passable gradually only by cold tolerant forms.

The fact that many of the recent arrivals in North America are congeneric or conspecific with Old World forms seems to indicate dispersal in the late Tertiary or Quaternary. The development of secondary centers of evolution in tropical and subtropical regions of the New World is explained by the early isolation of these regions from those of the Old World due to the fragmentation and northward displacement of Laurasia and parts of Gondwana.

Conclusions.—The dispersal of the Old World Element can be explained by the sole use of the Bering bridge. It is reasonable to question, however, whether it could have been used by all of the early immigrants since the distribution of some of these groups suggests a tropical center of origin. The dispersal of the Old World Element can also be explained by the concept of drift. From the standpoint of drift there would be no difficulty in explaining the dispersal of tropical forms.

THE NORTH AMERICAN ELEMENT

Mayr's data and interpretations.—During the Tertiary the greater part of North America had a subtropical or tropical climate, and for most of that period it was separated from South America and connected with Asia only by the Bering Strait bridge. There developed during this period a fauna which was classified as partly "holarctic" and partly "neotropical," but which is evidently a separate element that originated in North America. Tropical families and genera are well represented in this Element (table 6). For those groups that reached South America, the chain of islands that stretched from Colombia to Central Mexico was the route of dispersal. For those groups that reached Eurasia, Bering bridge was the route of dispersal.

TABLE 6.—NORTH AMERICAN ELEMENT

Cathartidae: New World vultures	Mimidae: mockingbirds
Tetraonidae: grouse	Polioptilinae: gnatcatchers
Odontophorinae: American quail	Bombycillidae: waxwings
Meleagrididae: turkeys	Ptilogonatidae: silky flycatchers
Aramidae: limpkins	Dulidae: palm-chats
Todidae: todies	Vireonidae: vireos, shrike-vireos, pepper-shrikes
Momotidae: motmots	Parulidae: wood warblers
Cinclidae: dippers	Emberizinae: typical buntings
Troglodytidae: wrens	

[Some genera and species belonging to the families listed in table 2 (hawks, nightjars, woodpeckers, swallows), in table 3 (trogons, barbets), and in table 5 (cuckoos, typical owls, pigeons, jays, thrushes, titmice, wren-tit, cardueline finches) are distinct enough to require mention under this heading.]

Commentary.—For all of the Elements discussed thus far the question has been the routes of dispersal into North America. Since we are now dealing with an autochthonous North American fauna the question is the routes of dispersal to other continents, for some members of this fauna have dispersed to Eurasia (*e.g.* Tetraonidae), or to South America (*e.g.* Mimidae, Paruli-dae), or to both (*e.g.* Cinclidae, Troglodytidae, Bombycillidae, Emberizinae).

With regard to the dispersal into Central and South America, there is no serious problem because of the general similarity in climatic conditions. There may be some question about the place of origin for some of the groups in this Element, as Mayr states, but whether the groups arose in North America or South America the route of dispersal was unquestionably the same. For those groups that dispersed into Eurasia the Bering Strait bridge could well have been the route of dispersal. The few forms that reached Eurasia are either cold tolerant or seem to have wide climatic tolerance.

North American Element from the standpoint of drift.—According to the theory of drift, the North American fauna could have dispersed southward through the Central American archipelago. The dispersal into Eurasia could have taken place across the North Atlantic connection, or across the Bering Strait bridge.

Conclusions.—The dispersal of forms from North America to Eurasia and/or South America can be explained by either the theory of permanence or the theory of drift.

THE PAN-AMERICAN AND SOUTH AMERICAN ELEMENTS

Mayr's data and interpretations.—These Elements are considered separately by Mayr, but are combined here because the problem in each case is similar.

A number of American families are so rich in endemic genera and species in both North and South America that it is impossible to determine their place of origin without fossil evidence. These families were able to utilize islands as stepping stones from one continent to the other, and because of the similarity in climate it was relatively easy for these groups to extend their ranges between tropical South America and southern North America, and vice versa. These extensions of range probably took place prior to the connec-tion of the two continents in late Pliocene. Four families (table 7), almost certainly South American in origin, are rich in species and have at least a few species in temperate North America, yet not one of these families has crossed

TABLE 7.—Pan-American Element

APPARENTLY ORIGINALLY NORTHERN	
Cracidae: curassows, guans	
PROBABLY ORIGINALLY SOUTH AMERICAN	
Tyrannidae: tyrant flycatchers	Thraupidae: tanagers
Trochilidae: hummingbirds	? Icteridae: blackbirds, troupials

[The cardinals (Richmondeninae) may have to be transferred from the South American group to this class.]

TABLE 8.—South American Element

*Rheidae: rheas	Ramphastidae: toucans
Tinamidae: tinamous	Dendrocolaptidae: wood-hewers
*Anhimidae: screamers	Furnariidae: oven-birds
*Opisthocomidae: hoatzins	Formicariidae: antbirds
*Psophiidae: trumpeters	Conopophagidae: ant-pipits
*Eurypygidae: sun-bitterns	Rhinocryptidae: tapaculos
*Cariamidae: cariamas	Cotingidae: cotingas
*Thinocoridae: seed-snipe	Pipridae: manakins
*Steatornithidae: oil-birds	*Oxyruncidae: sharp-bills
Nyctibiidae: potoos	*Phytotomidae: plant-cutters
Galbulidae: jacamars	Coerebidae: honey-creepers
Bucconidae: puff-birds	Richmondeninae: cardinals

[Families marked with an asterisk contain less than five species, and their allocation is consequently somewhat doubtful. In most cases it is well supported by circumstantial evidence.]

Bering Strait into the Old World. Birds of Old World origin that arrived in North America at an early date and then crossed to South America include the pigeons (Columbidae), the gnatcatchers (Polioptilinae), some thrushes (Turdinae), and some cardueline finches. From Mayr's discussion of the Cuculidae under the Old World Element, it would seem that it also belongs in this group.

In contrast to the families in the Pan-American Element which have endemic genera and species in North America, the families of the South American Element (table 8) are extremely rare, or completely lacking north of the tropics. As a rule, these families are richly developed in all parts of South America, even in the tropical parts. The families comprising the ant-bird (Formicariidae), the oven-birds (Furnariidae) and woodhewers (Dendrocolaptidae) are even more restricted to South America, none of them having reached the West Indies.

"It is most remarkable that none of the families that are clearly South American in origin has developed any species that have crossed into the Old World.* Old World families, on the other hand, have sent many branches into South America" (p. 26). Of the four Pan-American families of probable South American origin (Trochilidae, Tyrannidae, Thraupidae, and Icteridae) "not one . . . has crossed Bering Strait into the Old World although all four are rich in species and all four have at least a few species in temperate North America, some extending even as far as Alaska" (p. 24).

Commentary.—The interpretation of the origin and dispersal of the Pan-American and South American Elements is adequate to account for the faunal similarities of the Americas.

By raising the question of why none of the South American families has developed any species that have crossed into the Old World and not being able to answer it convincingly, I think Mayr unjustifiably weakens his interpretations of some of the other faunal elements. Because the Bering bridge has been used so freely to explain dispersal to the New World, it does seem remarkable that none of the South American families has crossed into the Old World, but this type of negative reasoning must be applied with great caution. Be-

* The Myrtle Warbler (*Dendroica coronata*) and the Northern Water-thrush *Seiurus noveboracensis*) have recently crossed into the Anadyrland (Mayr, p. 38).

cause a land connection exists, it does not follow that a fauna, or parts of it, can be expected to disperse through it. Other factors in dispersal should not be minimized or overlooked.

If one accepts only the Bering Strait bridge as the route of dispersal between the Old and New worlds, then it follows that Bering bridge was a highly selective, essentially *one-way bridge*. It is difficult to find an adequate explanation for such a condition that is consistent with the interpretations of the origin of the other faunal elements. Mayr suggests (p. 26): "Perhaps this means that a temperate zone family can more easily become adapted to the tropics than a tropical family to a temperate climate." At present it would seem more desirable to reason from known cases of dispersal rather than attempt to explain failure to disperse. In any case, the use of negative evidence in this instance appears to weaken interpretations based on the sole use of Bering bridge and does not seem justifiable.

Pan-American and South American Elements from the standpoint of drift.—From the standpoint of drift these faunas (except the Cracidae) are interpreted as originating and evolving in South America, with some forms dispersing into North America. This dispersal began possibly before the separation of North America and South America in the Eocene and it continued throughout the Tertiary. The route of the dispersal was the Central American archipelago and the direct land connection when it was present.

Conclusions.—The distribution of the Pan-American and South American Elements can be explained by either the theory of permanence or the theory of drift.

Discussion, Conclusions, and Summary

THE ORIGIN OF THE NORTH AMERICAN AVIFAUNA

Mayr's interpretation, based on permanence, may be summarized as follows:

1) North American families and subfamilies are a) Old World in origin; b) South American in origin; or c) North American in origin. 2) Some families that originated in North America dispersed, at least in part, to the Old World and to South America. 3) The avenue of dispersal between the Old World and the New World was the Bering Strait bridge. 4) The avenue of dispersal between North America and South America was the Central American archipelago or direct land connection. 5) If dispersal occurred at an early date, then a secondary center of evolution developed in the acquired area.

This interpretation is beset with a number of difficulties as follows:

1) It implies that all of the families of cosmopolitan distribution have dispersed through Bering Strait or by transoceanic colonization. 2) It states that Bering Strait was the only avenue of dispersal for the families of Pantropical, Panboreal, and Old World Elements, and a small part of the North American Element. When one combines these with the cosmopolitan families it is evident that more than a majority of the families and subfamilies of the World are presumed to have crossed Bering Strait. 3) The great use of the Bering bridge by so many diverse forms would require a wide range in ecological conditions at any one period and/or in successive periods. That the Bering bridge supported such diverse ecological conditions appears unlikely when one accepts the inclination of the earth's axis to the ecliptic as a stable feature in geological history. 4) It fails to explain adequately the distribution of the Pantropical families, and especially the distributon of similar

genera in the now widely separated land masses of the Southern Hemisphere. 5) It appears to be inconsistent, since it postulates that numerous Old World families (including some which are now wholly tropical) have crossed Bering bridge and reached South America, yet none of the South American and only a few of the North American families have crossed Bering Strait to the Old World.

Now let us summarize the interpretation based on drift, and then compare the two interpretations.

According to drift the American fauna can be derived as follows:

1. A large, older part from an *original* avifauna that dispersed readily through Gondwana and/or Laurasia in the late Cretaceous and early Tertiary. This part of the avifauna we may term the *Original Older Element*. It would include those groups in the Unanalyzed Element, the Pantropical Element, and the Old World Element which have extensive distributions.

2. A smaller part which developed (or survived) in northern North America and/or Eurasia and dispersed freely across the North Atlantic connection (and its remaining remnant, the Bering Strait "bridge"). Those families that developed here, (as opposed to surviving here) would comprise a younger element. This part (as a whole) we may term the *Holarctic Element*. (This would include those families in the Old World and North American Elements which are holarctic in distribution, and the Panboreal Element.

3. A third, and final part, which evolved in the New World, partly in the tropical southern half of North America and partly in South and Central America, with dispersal of several families in both directions. Included in this avifauna are a few old non-passerine families (perhaps survivors of, or not far removed from, the Original Older Element) and numerous passerine families. This element might well be termed the *New World Element*.

Thus, we have in North America 1) representatives of an old, original, widespread avifauna 2) representatives of an holarctic avifauna and 3) representatives of an avifauna that evolved in the New World. When there were originally two large land masses in close proximity with no major physical barriers and a relatively equable climate, much of the avifauna was probably cosmopolitan. After fragmentation and drift, two major changes appear: a) the isolation of the southern hemisphere land masses from each other and b) the gradual cooling of the northern portions of Laurasia as it drifted into higher latitudes. The gradual cooling and changing seasons in northern Laurasia and the failure of its fragments to become completely isolated could account for the development of the holarctic fauna. The isolation of South America and the tropical portion of North America (the former a physical isolation, the latter a climatic one) would have permitted the development of a New World fauna, which with a few exceptions, has not reached the Old World.

When we compare this interpretation with that based on permanence we find some features in common. Both postulate the existence of a New World Element. Both recognize the exchange of forms between the Old World and the New World and the need for some bridge or connection to explain the exchange. Both agree in the use of the Bering Strait bridge during the Tertiary and Recent periods. Where they differ markedly is that "permanence" uses only the Bering Strait connection and "forces" all exchanges into one pattern, while "drift" postulates broad intercontinental connections between the Old and New worlds and the gradual disruption of these connections. Therefore, some of the objections raised above to the interpretations based on perma-

nence are not met when drift is assumed. For example, according to *drift*, it is not necessary to assume that all forms (except obvious transoceanic colonizers) that have widespread distributions have dispersed through Bering Strait, or that tropical groups dispersed through "temperate" regions which had presumably arctic and subarctic conditions of day length. One may rightly argue that for each of the difficulties mentioned under permanence a possible explanation can be offered, as indeed has been done by its proponents, but in each case separate and new factors need to be postulated.

It cannot be stated too strongly or too often that permanence is only one of several theories of the evolution of the continents and ocean basins. Drift is another theory, and there are several others. On the whole, there is as much geological evidence for permanence as there is for drift, but in neither case is it incontrovertible. According to Umbgrove (1947), "the question of the origin of continents and oceanic depressions still remains an unsolved problem" (p. 254).

THE PROBLEM OF CENTERS OF DISPERSAL

The prevailing thesis among many American zoogeographers and phytogeographers is that of Matthew (1939). According to Matthew, 1) the principal lines of migration for land vertebrates in later geological epochs have been radial from holarctic centers of dispersal and 2) the geographic changes required to explain the present distribution of land vertebrates are not extensive; the permanence of the oceans as defined by the continental shelf is assumed, and the only land bridge, therefore, that was an avenue of dispersal between the Old and New worlds was at Bering Strait. Matthew's thesis was developed primarily on the basis of mammals, but he found it applicable to amphibians, reptiles, birds, invertebrates, and presumably plants. It was his contention that "no hypothesis can be finally accepted that does not conform to the facts of distribution in all groups of animals and plants. It is not a matter of preponderant evidence" (1939, p. 131).

The question of whether the primary centers of dispersal for many organisms were holarctic or tropical (or in the Southern Hemisphere) is an important one. The answer has a direct bearing on the problem of continental history, for if the centers of dispersal were tropical then the premise that the Bering Strait bridge was the only one between the Eastern and Western hemispheres becomes, in my opinion, less probable.

It is unlikely that there will be only *one* solution that will apply to *all* groups as Matthew contended. Nevertheless, it seems reasonable to assume that because of their interdependence the distribution patterns of many major groups of plants and animals should be explicable on generally similar grounds. In view of Matthew's contention that he found his hypothesis applicable to other groups of organisms, there are presented below the results and conclusions of some recent studies that are not entirely corroborative. These studies suggest strongly that the tropics and the Southern Hemisphere have been important centers of origin and dispersal, and they bring into sharp focus the problem of routes of dispersal.

Darlington (1948) analyzed the geographical distribution of the cold-

blooded vertebrates and came to the conclusion that they dispersed from the tropics and not from the Holarctic. He states (p. 105): "Fresh-water fishes, amphibians, and reptiles, seem all to have dispersed from the tropics into the north temperate zone, more than the reverse. . . . The north temperate zone, especially its colder part, is apparently not a great center of evolution of cold-blooded vertebrate life, but a marginal area where such life is limited." Darlington, furthermore, questions Matthew's theory of the effect of climate on evolution, but agrees that it is not necessary to "remodel the world" to account for vertebrate distribution.

Camp (1947) studied the distribution patterns of angiosperms in relation to basic phyletic phenomena and concluded that such studies point "rather directly to a southern origin of the angiosperms" (1947, p. 183). Camp states further: "Naturally, such a sequence of events will demand a former somewhat different (but I think geologically not impossible) alignment of the land masses of the Southern Hemisphere than now exists." In a later study (1952) of phytophyletic patterns on lands bordering the South Atlantic Basin, Camp concluded that various groups arose in the Southern Hemisphere probably in pre-Cretaceous time, and underwent further evolution entirely within the Southern Hemisphere. The phyto-phyletic relationships between Africa and South America "defy rationalization on the basis of essentially static land areas and postulated normal climatic zonations."

On the other hand, Just (1947) holds to a northern origin of anigosperms and concludes that a modified form of the theory of continental drift may prove acceptable if shown to be connected with diastrophism. Later (1952), when considering the fossil floras of the Southern Hemisphere and their bearing on continental drift, he states: "Although the oldest fossil angiosperms known so far were found in Greenland, some of their forerunners may well have been present in the Southern Hemisphere. . . . Antarctica is generally recognized as an important center of origin and dispersal, and the Pacific Ocean is regarded as older than the Atlantic."

Regarding the problem of the alignment of the land masses in the Southern Hemisphere, Caster (1952), after re-examining the paleontology and stratigraphy of South Africa and southern South America, states: ". . . The paleontologic and stratigraphic parallelism of the middle and late Paleozoic and early Mesozoic . . . seem to require until the close of the Triassic, either a trans-oceanic bridge of continental characteristics, or the proximity of the two present land masses. . . . There is no wholly acceptable explanation of these Afro-American similarities; currently both 'bridging' and 'drifting' are equally respectable working concepts and the truth may ultimately comprise certain characteristics of both."

These recent studies make it clear that many biogeographic problems require reëxamination and re-orientation.

In the present paper only one of several geological theories has been used to reëxamine the problem of the origin of the North American avifauna. Another one that might well be used is that of foundering. Surely, present studies in biogeography cannot avoid the use of the multiple geological hypotheses of permanence, drifting, and foundering. It is not at all unlikely that all three have played a rôle in the evolution of the continents and ocean basins.

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The Nesting of the Four-Toed Salamander, Hemidactylium scutatum (Schlegel), in Virginia

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Reported here are observations on the nesting of the four-toed salamander, *Hemidactylium scutatum* (Schlegel) in Virginia. This species is frequently regarded as rare in areas where its nesting has not been investigated. Prior to this report it was so considered in Virginia, and less than a score of adult specimens from this state were found in the collections of the major museums. During this survey data were obtained on 224 nests in 21 localities in 13 of the 100 counties of Virginia.

Suitable nesting areas for *Hemidactylium* are abundant on the Virginia coastal plain. The large numbers of specimens found in the few habitats explored are evidence of the abundance of this species in eastern Virginia. The population of *Hemidactylium* appears to rank fifth in size in this region, exceeded in numbers only by *Eurycea b. bislineata* (Green), *Desmognathus f. fuscus* (Raf.), *Diemyctylus v. viridescens* (Raf.), *Plethodon c. cinereus* (Green) and their indigenous subspecies and intergrades.

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Nesting habitats.—All nesting habitats had two characteristics in common —slow-moving or still water, and material in a site adjacent to the water in which eggs could be concealed. A wide variety of habitats met these conditions. Nests were found in mosses, sedges, hepatics, under loose bark, in mounds of pine needles, and in rotten wood. Most of the nests were found in or under mosses. The relationship of the egg-group to the moss depended on the presence or absence of natural crevices in the moss. The deep, or "thick" mosses formed loose, bushy masses containing many natural crevices into which eggs could be deposited, while the shallow, or "thin" mosses offered few crevices, but often served as the cover of shallow depressions in earth or rotted wood. In habitats having both "thick" and "thin" mosses, nests were generally found only in the former.

Nests were found in the 18 localities in fig. 1. Nesting was also observed in three other localities: Appomattox County, 2 miles NNW of Appomattox Court House; Charlotte County, ½ mile north of Phoenix; and Fairfax County, between New Alexandria and Dyke (reported by J. A. Fowler in personal letter, March 25, 1950).

Nests have been found by meandering, shallow bog streams, by ponds, by

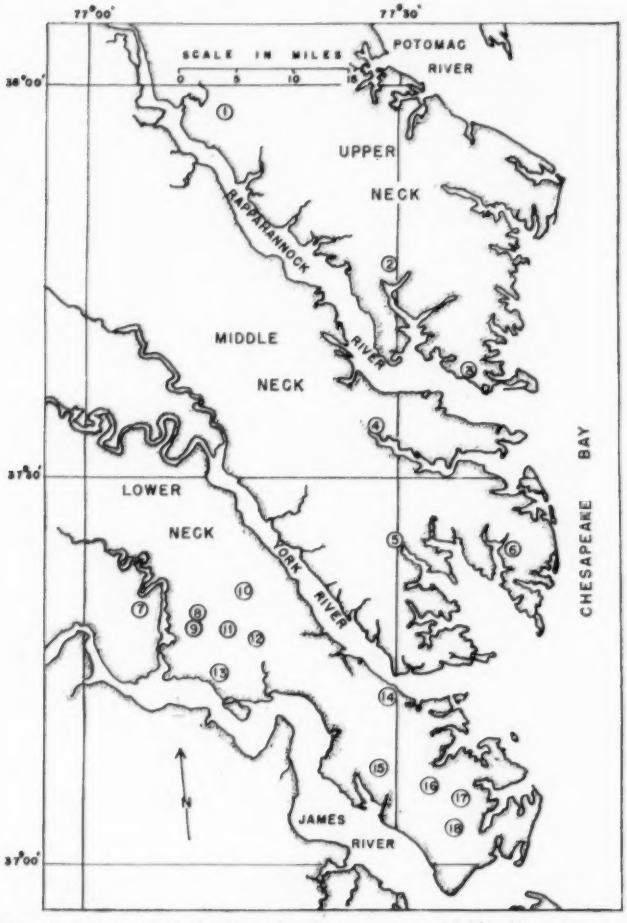

Fig. 1.—Locations of the *Hemidactylium scutatum* (Schlegel) nesting sites found on the Virginia coastal plain

LEGEND: 1. Richmond Co., 4 mi. WSW of Warsaw; 2. Lancaster Co., Lively; 3. Lancaster Co., ½ mi. N of Gray's Point; 4. Middlesex Co., 3 mi. S of Saluda; 5. Gloucester Co., 2 mi. NE of Gloucester Court House; 6. Mathews Co., ½ mi. SE of Mathews; 7. Charles City Co., 4 mi. SSE of Holdcroft; 8. James City Co., 2 mi. NE of Jolly Pond; 9. James City Co., ¾ mi. W of Jolly Pond; 10. York Co., 2 mi. NE of Lightfoot; 11. James City Co., 4 mi. NW of Williamsburg; 12. York Co., ½ mi. N of Williamsburg; 13. James City Co., ½ mi. W of Five Forks; 14. York Co., Yorktown area; 15. Warwick Co., 1½ mi. E of Denbigh; 16. Warwick Co., ½ mi. E of Harpersville; 17. Elizabeth City Co., Buzzard's Roost area; 18. Elizabeth City Co., Fox's Store area.

seepage springs, and adjacent to stagnant pools in drainage ditches and brooks. Most nests are found between three and eight inches from the water surface (Bishop, 1920; Blanchard, 1922). Water adjacent to the nests varied in depth from a fraction of an inch to several feet.

Twice in this survey egg groups were found isolated from surface water areas by several feet of mud. On March 24, 1940 a nest in a wooded ravine 2 miles NE of Gloucester Court House was found in a thick layer of *Thuidium delicatulum* (Hedw.) Mitt., in a shallow depression on the top of a large log lying three feet from the nearest water. On March 25, 1950 three nests were found in a wooded ravine 2 miles NW of Lightfoot, in a moss growth on a bank more than ten feet from surface water. In both cases these nests were probably adjacent to water areas during rainy periods.

The water areas beside nests are rarely muddy, and are usually clear and still. They may be colorless, green with algae, or the typical black water of cypress swamps. Several nests were found near moving water in bogs. The flow-rate of these bog streams was found to not exceed 0.2 miles per hour; heavy rains undoubtedly would temporarily markedly alter this flow-rate. The mean of five pH determinations in a cypress pool *Hemidactylium* habitat near Five Forks was 5.0 on March 27, 1950.

Nests are reported in deciduous biomes (Bishop, 1920; Blanchard, 1922). In Virginia in addition they are found in coniferous woods. Egg groups have been found in pond vicinities in the proximity of the following types of trees: cypress, *Taxodium distichum* (L.); loblolly pine, *Pinus taeda* L.; holly, *Ilex opaca* Ait.; sycamore, *Platanus occidentalis* L.; beech, *Fagus grandifolia* Ehrh.; white oak, *Quercus alba* L.; and chestnut oak, *Q. prunus* L. Several habitats lacked trees.

Although Hughes (1886) first noted *Hemidactylium* eggs in moss, it remained for Bishop (1920) to identify eggs with sphagnaceous habitats. Gilbert (1941) also found nests in *Sphagnum*, and in addition reported nests in mosses of several other genera: *Climacium, Mnium,* and *Thuidium*. Nests have been found in Virginia in mosses of these four genera and nine others: *Atrichum, Aulacomnium, Cirriphyllum, Entodon, Eurhynchium, Hypnum, Leptodictyum, Leucobryum,* and *Plagiothecium*. Nests are often found in hummocks consisting of mosses of several genera, sedges of the genus *Carex*, and occasionally hepatics. The following genera of *Hepaticae* were involved: *Lophocolea, Pallavicinia, Scapania,* and *Teleranea*. The mosses and hepatics in nesting sites, and the number of nests associated with them, are compiled in table 1.

A few nests are found in other habitats. Blanchard (1922) noted some nests in southern Michigan habitats in crevices in the sides of rotted, water-soaked logs, and under the loose bark of stumps. Of the 224 nests examined in Virginia, 175 were in crevices among the leaves and stems of mosses, sedges, and hepatics; 40 were suspended from the rhizoids of moss and roots of sedge over crevices in rotted logs and eroded banks; and nine were in the unusual habitats listed below:

No. of Nests	Habitat	Counties
4	Inside of rotted planks, boards, and logs	James City, Mathews, Lancaster, and York
2	Under loose bark on logs and stumps	Elizabeth City
2	In damp mounds of pine needles and strips of bark	James City
1	In hollow cypress knee	James City

Egg-laying.—Egg-laying in eastern Virginia begins seven weeks earlier than it does in southern Michigan (Blanchard, 1934b) and New York (Bishop, 1941). The earliest date on which nests have been found in Virginia is February 24, 1951, when three egg groups were collected near Five Forks.

The egg-laying period in Michigan lasts two weeks, extending from mid-April to May (Blanchard, 1934b). In Virginia, in the Williamsburg area, it lasted for two weeks in 1951, starting on February 24th, and ending on March 10th. On February 24th four of every five females were gravid, and had all of their large ova still confined to their ovaries (undistended oviducts); on March 4th only one in six females remained in this condition. By March 10th only one in 50 females was found to still have all large ova confined to the ovaries.

Egg-laying can occur beyond the limits of the nesting season defined above. On March 4, 1951 Mr. O. K. Goodwin collected 22 hatching eggs near Denbigh; if a 60 day incubation period is assumed, these eggs must have been deposited during the first week of January. Incubation time varies inversely with temperature, and it is more likely that these eggs were deposited in late November or December, 1950.

Bishop (1941) reported that *Hemidactylium* eggs are deposited in nest cavities which often have the appearance of having been formed by turning movements of the females, but that sometimes it was quite clear that the females had merely exploited natural crevices in the mosses. All of the nests examined in this study apparently resulted from the utilization of natural crevices by the females, and the shape of these crevices often determined the scatter and shape of the egg group. The outer envelopes of recently deposited eggs are adhesive, and as they are deposited the adjacent eggs adhere in compact clusters in the spacious crevices in loose clumps of "thick" mosses like *Thuidium*. In the "thin" mosses like *Plagiothecium* and *Cirriphyllum* there is a lack of large crevices that could house a compact group of eggs, and the eggs are attached to the rhizoids in a compact single layer.

Blanchard (1922) reported that the eggs are placed "either just under the moss covering of an old stump or root, or entangled in moss rhizoids and grass roots, not in the earth below the roots nor in the moss and grass above the roots. In Virginia 78 per cent of the nests were found among the shoots and leaves, entirely above the roots, in mixtures of mosses, sedges, and hepatics. The other 18 per cent of the nests were attached to rhizoids as described by Blanchard (*ibid*) or were in unusual habitats. Nests were attached to rhizoids and roots in habitats in which the moss cover was thin, as in the *Cirriphyllum* habitat in Appomattox County.

Crevices in mounds of pine needles, in rotted logs, and under loose bark were usually too small for the deposition of compact clusters of eggs, and in these habitats nests were frequently spread over large areas in a single or double layer. These confining habitats did not prevent numbers of females from depositing their eggs in a few large common nests. Separate nests of 528 and 438 eggs were found in mounds of pine needles, and one composite nest of 284 eggs was found under loose bark.

Bishop (1941) noted that *Hemidactylium* turns "upside down" when depositing eggs. This behavior is characteristic of a number of species of Plethodontidae that deposit their eggs in water, attaching them to the lower surface of some support. Similar behavior has also been observed for several species of salamanders that deposit their eggs in terrestrial situations. In Virginia the four-toed salamanders only follow this behavior pattern under certain conditions, i.e. when they deposit their eggs in loose moss hummocks containing large natural crevices. Where freedom of movement is more limited, as in confining crevices such as beneath loose bark, the position of the female during egg deposition is variable, largely determined by the available space in the habitat being utilized. Vertically oriented nests have been found on the vertical surfaces of boards surrounding springs, with the eggs attached to the board in a single layer at the base of a shallow growth of moss. Females have not been observed in the process of laying their eggs in these nests, but the "upside down" position cannot account for the egg placement. In the laboratory, on two occasions, females have been observed depositing eggs on the vertical walls of glass jars, while "standing on their heads" in their orientation to an horizontal surface. These females were held against the glass by adjacent moss, and were in vertical positions with their heads downward. After depositing an egg they would move a fraction of an inch down the side of the jar, and deposit another, an egg-deposition behavior probably utilized in vertical nests.

On March 23, 1950 near Yorktown, and on March 4, 1951 near Denbigh, eggs were found deposited in the open, on top of moss hummocks. In both of these instances the hummocks contained large numbers of eggs representing the egg complement of eight to fourteen females, and all natural crevices in the mosses were already jammed with eggs. These exposed eggs were undoubtedly deposited by females in a "right side up" position, with their ventral surfaces toward the earth.

In many nesting sites insular groups of eggs were found in mosses on floating logs, cypress knees, or sedge hummocks isolated from the pond shore by several feet of water, — locations available only to females that swim in their spring migration as reported by Blanchard (1934a). On March 27, 1950, 28 nests were counted around the pond at Five Forks; 19 of these were on little islands, four others were on logs extending out into the pond several feet from the shore line, and the remaining five were found along the bank. Many of these nests were unattended by females.

Incubation period.—Bishop (1941) reports that the incubation period is variable, and depends on temperature, moisture, "and perhaps other factors." Field observations of egg-laying and hatching in New York show that the incubation period requires from 52 to 60 days (Bishop *ibid*). One egg-group observed as it was being deposited on March 4, 1951 near Five Forks was found with the larvae emerging on May 3, 61 days later.

No data on the temperature of nests and adjacent air and water were found in the literature. Nest temperatures were measured with the thermometer bulb in contact with the eggs; air temperatures were measured five centimeters above the nest hummocks, and water temperatures were taken adjacent to the nests. Temperatures in a group of nine nests near Five Forks were checked on March 25, 1950, as follows:

NEST NO.	AIR TEMP. °C.	NEST TEMP. °C.	WATER TEMP. °C.	GENUS OF MOSS AROUND EGGS
1	31.0	24.5	21.5	Thuidium
2	27.0	24.0	21.0	Thuidium
3	29.5	24.0	22.0	Thuidium
4	29.5	25.0	23.0	Thuidium
5	29.0	23.5	22.5	Thuidium
6	28.0	24.0	23.0	Thuidium
7	28.0	23.0	21.0	Thuidium
8	29.0	21.0	21.0	Sphagnum
9	28.0	19.0	21.0	Sphagnum

Temperatures in the seven *Thuidium* habitats were higher than those in the two *Sphagnum* habitats; further studies are needed to determine the degree to which these differences prevail during the incubation period, and the extent to which they influence the rate of egg development.

Relation of Hemidactylium nesting to other spring events.—Blanchard (1922) points out two spring events in southern Michigan that coincide with the egg-laying of *Hemidactylium:* hepaticas (*Hepatica triloba* Chaix) begin blooming, and spring peepers (*Hyla c. crucifer* Wied) begin chorusing. Neither of these events coincided with *Hemidactylium* egg-laying in Virginia in 1950 and 1951. Hepaticas were blooming a month earlier, when *Eurycea bislineata b. X cirrigera* were beginning egg-laying, and the spring peepers failed to peep until two weeks after egg-laying of Four-toes had begun. It was noted that spring beauty (*Claytonia virginica* L.) and bloodroot (*Sanguinaria canadensis* L.) made their first appearances when *Hemidactylium* began laying eggs.

Blanchard (1934b) further notes that Michigan *Hemidactylium* emerge from hibernation "many days, perhaps three weeks, after the spotted salamanders have mated and laid their eggs." In 1951 in the Williamsburg area both *Ambystoma maculatum* and *Hemidactylium* deposited most of their eggs in the period from February 24th through March 10th.

Summary.—*Hemidactylium scutatum* (Schlegel) is a common salamander on the Virginia coastal plain.

Nests are usually situated within a few inches of still or slowly moving water, in crevices in hummocks of mosses, hepatics, and sedges.

Nests are found in deciduous and coniferous woods; cypress, loblolly pine, holly, sycamore, beech, white oak, and chestnut oak have been noted in nesting areas.

Eggs are found in mosses of several genera: *Atrichum, Aulacomnium, Cirriphyllum, Climacium, Entodon, Eurhynchium, Hypnum, Leptodictyum, Leucobryum, Mnium, Plagiothecium, Sphagnum,* and *Thuidium.* The suitability of a moss as a nesting site appears to be determined by its proximity to water and the pressure of natural crevices among its shoots and rhizoids, or under them.

Nests are frequently found in hummocks composed of several mosses, species of sedges (*Carex*), and occasionally hepatics of the following genera: *Lophocolea, Pallavicinia, Scapania,* and *Teleranea.*

A few nests have been found in mounds of pine needles, inside of rotted logs and boards, under loose bark, and in hollow cypress knees.

February 24, 1951 is the earliest date on which eggs have been found; this is approximately seven weeks earlier than the reported initiation of nesting in New York and Michigan.

Egg-laying is accomplished in a two-week period in Michigan; the majority of egg-laying in Virginia occurs in a period of similar duration.

An instance of off-season egg deposition, involving a nest of hatching larvae collected on March 4, 1951, is reported.

Virginia *Hemidactylium* nests do not appear to be found by the turning movements of the females; egg-distribution in nests points to the utilization of natural crevices for nesting sites.

In Michigan eggs are reported attached to rhizoids and roots; in Virginia nests are placed above the rhizoids and roots in 78 per cent of the nests, and suspended from the rhizoids in about 20 per cent.

Composite nests of 528, 438, and 284 eggs were found in confining spaces in mounds of pine needles and beneath bark.

Females usually deposit their eggs while in an "upside down" position; in vertically oriented nests they may deposit eggs while "standing on their heads," and in two cases eggs were found on top of moss hummocks indicating that in some cases females deposit eggs while in a "right side up" position.

Some nests were located on banks of ponds; many were located on islets in pools, in locations only attainable by swimming females.

An incubation period of 61 days was noted for one nest in the Five Forks area of James City County in 1951.

Nest temperatures in two *Sphagnum* habitats were lower than those in seven *Thuidium* hummocks at the same nesting site.

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TABLE 1.—Mosses and hepatics surrounding *Hemidactylium* nests

COUNTY AND LOCALITY	NO. OF NESTS	SPECIES OF MOSSES AND HEPATICS
Appomattox: 2 mi. NNW of Appomattox	31	*Cirriphyllum boscii* (Schwaegr.) Grout, *Thuidium delicatulum* (Hedw.) Mitt.
Charles City: 4 mi SSE of Holdcroft	2	*Climacium kindbergii* (R. and C.) Grout, *Hypnum patientiae* Lindb., var. *demissum* Schimp., *Mnium cuspidatum* Hedw.
Charlotte: ½ mi. N of Phenix	5	*Entodon seductrix* (Hedw.) C. Muell., *Eurhynchium serrulatum* (Hedw.) Kindb., *Mnium cuspidatum* Hedw., *Thuidium delicatulum* (Hedw.) Mitt.
Elizabeth City: Buzzards Roost area	2	Unidentified
Elizabeth City: Fox's Store area	2	*Eurhynchium serrulatum* (Hedw.) Kindb.
Fairfax: Between New Alexandria and Dyke	1	*Sphagnum* (reported in letter by J. A. Fowler, March 25, 1950)
Gloucester: 2 mi. NE of Gloucester Court House	3	*Thiudium delicatulum* (Hedw.) Mitt.
James City: ½ mi. W of Five Forks	79	*Atrichum crispum* (James) Sull., *Climacium americanum* Brid., *Climacium kindbergii* (R. and C.) Grout, *Pallavicinia lyellii* (Hook.) S. F. Gray, *Scapania nemorosa* (L.) Dum., *Sphagnum imbricatum* Hornsch., *Sphagnum palustre* L., *Teleranea nematodes* (Aust.) Howe, *Thuidium delicatulum* (Hedw.) Mitt.
James City: ¾ mi. W of Jolly Pond	1	*Aulacomnium palustre* (W. and M. Schwaegr., *Leucobryum glaucum* (Hedw.) Schimp.
James City: 2 mi. NE of Jolly Pond	8	Unidentified
James City: 4 mi. NW of Williamsburg	1	*Sphagnum palustre* L.
Lancaster: ¼ mi. N of Gray's Point	5	*Hypnum patientiae* Lindb., *Leptodictyum riparium* (Hedw.) Warnst., *Leucobryum glaucum* (Hedw.) Schimp.
Lancaster: Lively	1	*Thuidium delicatulum* (Hedw.) Mitt.
Mathews: ½ mi. SE of Mathews	5	*Hypnum patientiae* Lindb. var. *demissum* Schimp., *Plagiothecium micans* (Sw.) Paris var. *fulvum* (Hook and Wils.) Paris
Middlesex: 3 mi. S of Saluda	5	*Climacium americanum* Brid., *Climacium kindbergii* (R. and C.) Grout
Richmond: 4 mi. WSW of Warsaw	2	*Cirriphyllum boscii* (Schwaegr.) Grout, *Hypnum molluscum* Hedw., *Thuidium delicatulum* (Hedw.) Mitt.

TABLE 1.—(*Continued*)

COUNTY AND LOCALITY	NO. OF NESTS	SPECIES OF MOSSES AND HEPATICS
Warwick: ½ mi. E of Harpersville	7	*Atrichum crispum* (James) Sull., *Climacium americanum* Brid., *Sphagnum imbricatum* Hornsch. var. *affine* (R. and C.) Warnst., *Thuidium delicatulum* (Hedw.) Mitt.
Warwick: 1½ mi. E of Denbigh	52	*Climacium americanum* Brid., *Climacium kindbergii* (R. and C.) Grout, *Entodon seductrix* (Hedw.) C. Muell., *Eurhynchium serrulatum* (Hedw.) Kind., *Hypnum curvifolium* Hedw., *Hypnum patientiae* Lindb., *Leptodictyum riparium* (Hedw.) Warnst., *Leptodictyum trichopodium* (Schultz) Warnst., *Leucobryum glaucum* (Hedw.) Schimp., *Lophocolea bidentata* (L.) Dum., *Lophocolea cuspidata* (Nees) Limpr., *Lophocolea heterophylla* (Schrad.) Dum., *Mnium cuspidatum* Hedw., *Pallavicinia lyellii* (Hook.) S. F. Gray, *Plagiothecium micans* (Sw.) Paris, *Sphagnum palustre* L., *Thuidium delicatulum* (Hedw.) Mitt., *Thuidium microphyllum* (Hedw.) Best
York: 2 mi. NE of Lightfoot	3	*Climacium americanum* Brid., *Mnium cuspidatum* Hedw.
York: ½ mi. N of Williamsburg	1	Unidentified
York: Yorktown area	10	*Thuidium delicatulum* (Hedw.) Mitt., *Sphagnum palustre* L.

An Investigation and Comparison of the Fish Populations of Two Farm Ponds[1]

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The present study involves two watershed ponds located in the same valley in proximity to each other (fig. 1). It appeared that these ponds offered very similar environments with the exception of the following differences: (1) The watershed of the upper pond was heavily pastured during the winter and spring and the water of this pond was particularly turbid during this part of the year. The watershed of the lower pond was fairly well protected and did not exhibit the degree of turbidity exhibited by the upper pond. (2) The upper pond had an area of ¼ acre while the lower pond had an area of a little over ½ acre. (3) The upper pond received some barnyard drainage and at least during the summer of 1950 and 1951 exhibited a bloom of filamentous algae. At this time, the lower pond did not exhibit any such bloom. (4) The upper pond was constructed in 1942 while the lower pond was constructed in 1945.

Fig. 1.—Two Southern Illinois watershed ponds located in the same valley in proximity to each other.

1 A study sponsored by the Department of Zoology and Graduate College of Southern Illinois University.

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3 The authors wish to express their gratitude to Mr. Charles V. Lamer for permission to use his ponds for experimental purposes and to Dr. A. M. Mark of the Southern Illinois University Statistical Service for his help in the calculations of growth data.

The present discussion concerns the analysis of the fish populations of the two ponds. An attempt is made to determine the possible causes of population differences.

PROCEDURE

The fishes of the two ponds were collected with a five per-cent emulsified rotenone solution. To facilitate application of the emulsified rotenone solution, it was diluted with five parts water. This mixture was distributed over the ponds. Mixing was accomplished with an outboard motor. The lower pond was poisoned September 30, 1950, and the upper pond was poisoned October 5, 1950. Collection and examination of the fishes was started as soon as they commenced surfacing. The data are, of course, subject to the errors involved in eliminating a population by poisoning. By tagging and then poisoning, Carlander and Lewis (1948) obtained an estimate of the magnitude of this error. The following percent recoveries were obtained: bluegill, —38; white crappie—14; largemouth black bass—33; black bullhead—80; golden shiner—91.

This error is of limited concern since the emphasis of the study is a comparison between two ponds, i.e., the error in estimate should be roughly the same for both populations.

Weight and length measurements were made of all the specimens that were taken while fresh. For the fishes that came up a day or more after the poisoning only length measurements were taken. Scales were taken from the third row below the lateral line, and even with the end of the pectoral fin. Age determinations and growth calculations were made by the scale method. For purposes of reading, the scales were mounted dry between two slides and wet with water. The bluegill of the lower pond was the only group for which the body-scale relationship could be calculated. The relationship was determined to be: Standard length $=3.3+2.1972$ Scale radius with a correlation coefficient of 0.998. For the crappie, green sunfish, warmouth, and largemouth black bass published body-scale relationships from other areas were used (Lewis, 1950). The coefficient of condition, K, was calculated individually for each fish. Length-weight relationships were calculated from ungrouped data.

The following species of fishes were taken from both ponds: bluegill, *Lepomis macrochirus* (Rafinesque); white crappie, *Pomoxis annularis* (Rafinesque); green sunfish, *Lepomis cyanellus* (Rafinesque); warmouth, *Chaenobryitus coronarius* (Bartram); largemouth black bass, *Micropterus salmoides* (Lacepede).

The fish populations of the two impoundments were similar. The bluegill and white crappie were the dominant species, and the green sunfish, warmouth, and largemouth bass were present in fewer numbers.

PARASITES

Careful parasitological examinations were made on six specimens each of white crappie, bluegill, and green sunfish.[4] Superficial examinations were done on 30 of each of these species as well as 15 each of warmouth and largemouth bass. There were no signs of parasitic infections found in any of the specimens.

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4 Dr. Reino Freeman of the Department of Zoology, Southern Illinois University cooperated in the parasitological examinations.

FISH POPULATIONS

The analysis of the two populations revealed several differences which are of interest. The area of the lower pond was about twice that of the upper pond and yet the poundage and number of fishes in the two ponds were approximately equal (table 1). Thus it appears that the upper pond had a carrying capacity of about twice that of the lower.

It is rather difficult to arrive at a definite conclusion as to the relative population densities of the two ponds. One must not only confine comparison to a species but must also confine it to a size within a species. If total numbers for a species are considered, the bluegill populations of the two ponds were of about equal densities. If, however, on the basis of their not being competitive, one does not consider the fish below 54 mm in length (mostly young-of-the-year), the density of the bluegill population of the upper pond is about twice that of the lower. In a similar consideration of the white crappie populations, the density in the upper pond appears to be about four times that of the lower. Similar conclusions can be arrived at for the green sunfish, warmouth, and largemouth bass populations. On the basis of this analysis one may conclude that the upper pond was more crowded than the lower even though it also appeared to have a greater carrying capacity.

Having in mind that the upper pond appears to have had a higher total

TABLE 1.—Population composition of two farm ponds in Southern Illinois. Calculated on basis of number and weight of fish per acre.

Species	SL range (mm)	Number of fish per acre		Total wt. in lbs. per acre	
		Upper	Lower	Upper	Lower
Bluegill	up to 54	152	938	0.8	4.4
	55-126	1668	692	101.2	60.0
	127 up	540	430	119.6	100.0
	Total	2360	2060	221.6	164.6
White crappie	up to 108	1032	110	37.6	4.8
	109-178	716	230	106.4	57.4
	179 up	84	.....	35.6	.....
	Total	1832	340	179.6	62.2
Green sunfish	up to 53	60	210	0.8	2.4
	54-116	60	90	4.0	5.4
	117 up	172	56	38.0	9.0
	Total	292	356	42.8	16.8
Warmouth	up to 84	16	56	0.8	2.8
	85-101	96	26	5.2	1.4
	102 up	156	44	18.4	5.2
	Total	268	126	24.4	9.4
Largemouth black bass	up to 110	.....	60	.....	3.6
	111-249	84	28	27.6	9.2
	250 up	12	14	20.4	19.0
	Total	96	102	48.0	31.8
Total		4848	2984	516.4	284.8

TABLE 2.—Calculated and measured lengths and weights. Sexes combined. Lengths expressed in millimeters and weights in grams.

A. Bluegill from Lamer's Upper Pond.

Age class	Number of specimens	Average calculated length at each annulus 1	2	3	4	Average at capture length	weight
I	24	34	....	.....	.....	85	24
II	8	36	73	.....	.....	105	41
III	7	33	75	104	.....	120	64
IV	11	36	73	101	125	140	101
Mean standard length[4]		35	74	102	125		
Equivalent total length		43	94	180	157		
Annual length increment[5]		35	39	28	24		
Annual weight increment[6a]		1.7	13.2	23.4	33.0		

B. Bluegill from Lamer's Lower Pond.

I	78	32	.....	.....	.....	97	37
II	58	34	100	.....	.....	133	94
III	42	34	91	125	.....	141	105
IV	10	25	80	111	131	140	108
Mean standard length[4]		33	95	123	131		
Equivalent total length		43	119	155	165		
Annual length increment[5]		33	62	34	20		
Annual weight increment[6b]		1.2	30.7	50.9	46.8		

C. White crappie from Lamer's Upper Pond.

I	10	59	.....	.....	.....	131	62
II	8	62	147	.....	.....	175	134
III	1	60	117	164	.....	200	188
IV	2	80	135	187	210	225	.....
Mean standard length[4]		62	142	179	210		
Equivalent total length		79	183	231	269		
Annual length increment[5]		62	77	50	23		
Annual weight increment[6c]		5.7	59.3	99.0	67.9		

D. White crappie from Lamer's Lower Pond.

I	6	72	.....	.....	.....	158	108
II	31	72	150	.....	.....	171	135
Mean standard length[4]		72	150				
Equivalent total length		94	193				
Annual length increment[5]		72	78				
Annual weight increment[6d]		9.5	79.7				

4 Weighted mean.

5 Derived from weighted mean SL of fishes that have grown through the particular year being considered.

6 Calculated for each annual length increment using length-weight relationship formula:

a. Log W= —4.322545+2.940366 Log L (Correlation coefficient=.994).
b. Log W= —4.649659+3.111696 Log L (Correlation coefficient=.994).
c. Log W= —4.645695+3.013715 Log L (Correlation coefficient=.998).
d. Log W= —4.702051+3.057147 Log L (Correlation coefficient=.990).

carrying capacity and that the population density of each species was greater in the upper pond, we may now consider the difference between the growth rate and coefficient of condition of the fishes from the two populations.

The bluegill of the lower pond exhibited a much higher length increment in the second and third years of life than did the bluegill from the upper pond (table 2A,B). The white crappie from the lower pond also appear to have grown more rapidly at least in their first year of life (table 2C,D). There doesn't seem to be any important difference between the growth of the other species from the two populations (table 3).

Coefficient of condition values (tables 3 and 4) indicate a strong difference between the two fish populations. The values of practically all size groups of bluegill were higher for the lower pond population. The same condition was also characteristic of the white crappie populations. The number of values for other species are probably not large enough to make any conclusion possible (table 3).

There was another condition of interest exhibited by these two fish populations. Young-of-the-year bluegill, bass, warmouth, and green sunfish were not well represented in the upper pond whereas young-of-the-year white crappie were strongly represented. This condition suggests that the turbid water of the upper pond was not favorable for bluegill, bass, green sunfish, and warmouth spawning, or it was not favorable for the survival of the young fish of these species. The white crappie apparently did not find the silt a detriment and their reproduction may have even been favored due to the reduction in competition. It has been previously observed that white crappie are characteristic of heavily silted waters (Eschmeyer, Stroud, and Jones, 1944; Lewis, 1950). A special ability to reproduce successfully in muddy waters might well be the explanation for the suspected dominance of the white crappie in such waters.

SUMMARY

Two watershed ponds in the same valley in proximity to each other were poisoned and an analysis was made of their fish populations. The two ponds appeared to be similar except for the following differences: 1) The upper pond

TABLE 3.—Annual length increments and coefficient of correlation, K, values for three species of fish from two farm ponds in Southern Illinois

Species	Average K	Length increments for each year of life				
		1	2	3	4	5
Green Sunfish						
Upper	3.20(5)[7]	35(14)	40(9)	29(3)	28(1)	
Lower	3.28(7)	39(7)	38(5)	37(2)	41(1)	
Warmouth						
Upper	3.28(2)	40(30)	31(30)	23(19)	19(7)	
Lower	3.72(3)	24(11)	28(8)	23(3)	.....	
Largemouth black bass						
Upper	2.29(5)	83(12)	94(2)	48(2)	42(1)	32(1)
Lower	2.23(6)	116(10)	78(4)	91(1)	.....	.....

[7] Numbers in parentheses indicate the number of specimens the calculations were based on.

TABLE 4.—Coefficient of condition, K, values for the bluegill and white crappie from two farm ponds in Southern Illinois

Length range in mm	*No. of Bluegill*		*Mean K-Bluegill*		*No. of Crappie*		*Mean K-Crappie*	
	Upper Pond	Lower Pond	Upper Pond	Lower Pond	Upper Pond	Lower Pond	Upper Pond	Lower Pond
30- 59	....	18	.....	3.53	....	....	.....	.....
60-109	27	58	3.64	3.73	11	9	2.40	2.62
110-159	20	128	3.59	3.88	7	6	2.44	2.63
160-209	....	.....	.....	.....	8	31	2.42	2.70
Total Specimens	47	204			26	46		
Mean K			3.62	3.81			2.42	2.66

was more turbid; 2) The upper pond had an area of one-quarter of an acre versus an area of one-half of an acre for the lower pond; 3) The upper pond received some barnyard drainage and during the summers of 1950 and 1951 exhibited a bloom of filamentous algae; 4) The upper pond was constructed in 1942, whereas the lower pond was constructed in 1945.

The differences found in the two populations were as follows: 1) On the basis of pounds of fish recovered per acre, the upper pond appeared to have about twice the carrying capacity of the lower pond; 2) The data indicated that the upper pond had approximately twice the population density of the lower pond; 3) The bluegill and white crappie of the lower pond in some years grew more rapidly than those of the upper pond; 4) The coefficient of condition values for the bluegill and white crappie of the lower pond were higher than the values for the fishes from the upper pond; 5) Young-of-the-year bluegill, largemouth bass, warmouth, and green sunfish were not well represented in the upper pond, whereas young-of-the-year white crappie were well represented.

No definite conclusions were drawn as to the possible correlation between the environmental differences and the population differences.

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Three New Intergeneric Hybrids of Cyprinid Fishes from Western Montana

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It has become well established that distinct species and genera of fishes hybridize naturally, particularly in the freshwater families Cyprinidae, Catostomidae, and Centrarchidae. The information accumulating about these crosses is helpful in determining the natural relationship of species, and is finding application in such fields as genetics, speciation, and wildlife management. There is a sizeable literature on fish hybrids. For treatment in detail of American cyprinid hybrids, see especially Hubbs and Schultz (1931), Shultz and Schaefer (1936), Raney (1940a, 1940b), Hubbs and Miller (1943), Hubbs (1951), and Hubbs and Bailey (1952). For catostomid hybrids see Hubbs, Hubbs, and Johnson (1943), Hubbs and Hubbs (1947), and Hubbs and Miller (1953). For centrarchid hybrids see Radcliffe (1914), Hubbs (1920), Hubbs and Hubbs (1931, 1932, 1933), Thompson (1935), and Bailey and Lagler (1938).

Among the fishes collected during two years in the Columbia River drainage of western Montana are three intergeneric minnow hybrids that have hitherto not been recorded. They are the crosses *Mylocheilus caurinum* × *Ptychocheilus oregonense*, *Ptychocheilus oregonense* × *Richardsonius balteatus*, and *Rhinichthys cataractae* × *Richardsonius balteatus*.[1] The hybrids were recognized as such by their intermediacy in characters that differentiate their parental species, and this was confirmed by other criteria, such as those discussed by Hubbs, Hubbs, and Johnson (1943). Their identifications were generously verified by Dr. Reeve M. Bailey of the University of Michigan Museum of Zoology.

Most of the measurements and counts in the comparing of the hybrids with the parental species were taken according to methods outlined by Hubbs and Lagler (1947). Procedures that do not follow the system of these authors are noted in the tables. The ratios of all measurements were made by mathematical division rather than by stepping over the surface. The hybrid index used in the tables and discussions is a means introduced by Hubbs and Kuronuma (1942) to express simply the relationship of the traits of the hybrid to those of the parental species. Each value for the one parental type is set at 0, and that of the other at 100. A Hybrid index of 50 denotes exact intermediacy between parental types. The recommendation is to set at 0 the value for the presumably more primitive of the parental species. *Mylocheilus* seems more primitive than *Ptychocheilus*, *Richardsonius* more so than *Ptychocheilus*, and *Rhinichthys* more so than *Richardsonius*.

[1] All material dealt with in this report is deposited in the Museum of Zoology of the University of Montana, with the exception of a few specimens of each type sent to the University of Michigan Museum of Zoology (UMMZ), and a series of yearling hybrids, *M. caurinum* × *P. oregonense*, which was borrowed from the University of Michigan Museum of Zoology.

Acknowledgements.—Most of the adult hybrids between *P. oregonense* and *M. caurinum* were collected by students attending the Montana State University Biological Station, Flathead Lake. I especially want to thank Dr. Royal B. Brunson, William Newman, Arthur Merrick, and Ruth N. Scott for watching for the specimens caught in their netting operations. Mr. Richard G. Bjorklund and Dr. Brunson kindly gave me information on the relative numbers of fish species and sexes taken at Flathead in the summer of 1951. This was from data being prepared for eventual publication by the Station. As previously acknowledged in this paper, Dr. Reeve M. Bailey of the University of Michigan verified the identification of the hybrids, loaned his collection of yearling *P. oregonense* × *M. caurinum*, and was otherwise cooperative and helpful. Dr. Carl L. Hubbs at Scripps Institution of Oceanography gave some of his valuable time to read the manuscript and, in his inimitable fashion, to offer many valued criticisms and suggestions.

MYLOCHEILUS CAURINUM × PTYCHOCHEILUS OREGONENSE

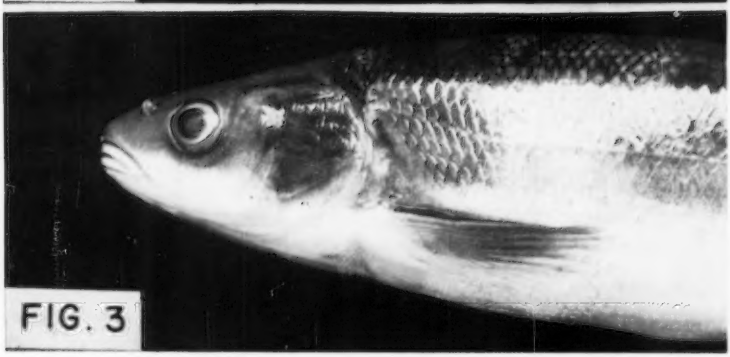
ADULTS FROM FLATHEAD LAKE

The most numerous hybrid taken was that of the Columbia River chub (*Mylocheilus caurinum*) crossed with the squawfish (*Ptychocheilus oregonense*). Twenty adults were gill-neted in Flathead Lake, Montana, during the summers of 1950 and 1951. The parental types are among the commonest native fishes in the lake. Apparently their spawning periods overlap, as milt and eggs could be stripped from both chubs and squawfish taken from the same nets during July and the first half of August.

Relative numbers of hybrids and of parental kinds.—From data available in field notes, the ratio of the collected hybrids to their parental species is amazingly high. On June 10, 1950, 25 chubs, 1 hybrid, and 20 squawfish were netted; and on June 24, 1 hybrid and 34 chubs. During the summer of 1951, 363 chubs, 16 hybrids, and 163 squawfish composed the minnow hauls. For all catches, the chubs make up 67.7 percent, the hybrids 2.8 percent, and the squawfish 29.3 percent. No cyprinid fishes other than the putative parental species were taken in the gill-nets. Species of other families included in these net hauls were *Salvelinus malma, Coregonus clupeaformis, Prosopium williamsoni, Catostomus macrocheilus,* and *Perca flavescens.*

COMPARISON OF THE HYBRIDS WITH THEIR PUTATIVE PARENTS

The chub is readily distinguished from the squawfish by its much smaller mouth, less dull coloration, presence of barbels, the blunt semimolar rather than sharp and hooked pharyngeal teeth, and by having 8 rays in the dorsal fin rather than 9. On superficial examination, the hybrids are more easily mistaken for squawfish than for chubs. Careful analyses, however, reveal them to be intermediate in almost all characters. A large number of counts and measurements were taken on the 20 hybrids and on 20 of each of the parental types. If the character proved not to be a critical one for the parental species, it was usually omitted. The parental specimens used for comparison all came from Flathead Lake; the majority were taken netted with the hybrids. Their size approximates that of the hybrids. The range in standard length of the chubs is 150-250 mm, with an average of 186.2 mm; the squawfish are 139-232 mm long, and average 179.3 mm; the hybrids are 160-214 mm long, and average 193.2 mm.



Figs. 1-3.—1. *Ptychocheilus oregonense*, head of a specimen 210 mm in standard length; 2. Hybrid (*Ptychocheilus oregonense* × *Mylocheilus caurinum*), head of a specimen 198 mm long; 3. *Mylocheilus caurinum*, head of a specimen 204 mm long. All specimens from Flathead Lake, Montana. Photographs by Jeanne Mueller.

Mouth and jaws.—In the chubs, the mouth is slightly oblique, the posterior margin of the upper jaw is curved, and it reaches only to below the anterior nares or the nasal septum. It is slightly overhung by the snout. The mouth of the squawfish is scarcely oblique, with no curve to the

upper jaw, and in adult specimens it reaches to below the anterior margin of the pupil or as far back as the posterior margin of the orbit. It is not overhung by the snout. The mouth of the hybrids is intermediate in size and shape. It is slightly oblique and reaches to below the posterior nares, or as far back as the anterior margin of the orbit. It is scarcely overhung by the snout, or is of equal projection (figs. 1-3). A measurement of the difference in mouth proportion, as determined by dividing the length of the jaw into the head length, is given in table 1. The relative size of the hybrid's mouth, with an index of 54, is almost exactly intermediate. In the range of variation, however, the proportions for the hybrids overlap those for the parental species.

Barbels.—Each of the chubs examined has a well-developed though small barbel at each jaw angle, whereas there are no barbels about the mouths of the squawfish. Of the 20 hybrids, 14 have no barbels, 4 have a rudimentary barbel on the right jaw only, 1 has a rudiment on the left side only, and 1 has a small barbel on each side.

TABLE 1.—Frequency distribution of the ratio of upper jaw length[2] to head length in hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense*, and in the parental species

	2.3-2.4	2.5-2.6	2.7-2.8	2.9-3.0	3.1-3.2	3.3-3.4	3.5-3.6	3.7-3.8	3.9-4.0	4.1-4.2	Ave.	Mean Dev.	Hybrid Index
Mylocheilus	....	....	....	....	4	....	6	4	4	2	3.65	0.25	
Hybrids	....	....	1	10	7	2	....	....	....	....	3.04	0.10	54
Ptychocheilus	6	11	2	1	....	....	....	....	....	....	2.51	0.09	

[2] The length of the jaw was taken from the tip of the snout to the posterior extremity of the left maxillary, with the mouth closed. It is not to be confused with the snout length, used as a character for the two other kinds of hybrids, which is the distance from the tip of the snout to the anterior margin of the orbit. The averages and the mean deviations were computed from the uncombined data.

Head.—The chubs have a relatively short and blunt head. The squawfish, on the other hand, has, for a cyprinid, a comparatively long head, giving it a pike-like appearance (fig. 1). The intermediacy of the hybrids in head length is well shown by proportional measurements (table 2).

Position of dorsal fin.—The position of the dorsal fin on the chubs is somewhat less posterior than on the squawfish. The distance from the origin of the dorsal to the last caudal scales when measured forward extends in the chubs to the tip of the snout, or as far anterior as 6 mm beyond the tip of the snout; in the squawfish, to the pupil or just in front of the nares; in the hybrids, to between the tip of the snout and the anterior margin of the nares. Again, the hybrids are almost perfectly intermediate in proportions (table 3). The overlap is small.

TABLE 2.—Frequency distribution of the ratio of head length to standard length in hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense*, and in the parental species

	3.3-3.3	3.5-3.6	3.7-3.8	3.9-4.0	4.1-4.2	4.3-4.4	4.5-4.6	Ave.[3]	Mean[3] Dev.	Hybrid Index
Mylocheilus	....	....	....	....	7	11	2	4.29	0.09	
Hybrids	....	....	5	9	6	....	....	3.96	0.12	49
Ptychocheilus	1	11	8	....	....	....	....	3.62	0.09	

TABLE 3.—Frequency distribution of the ratio (× 100) of the distance from the base of the dorsal fin to the tip of the snout, to that from the base of the dorsal fin to the end of scales on the caudal base, in hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense*, and in the parental species

	88-91	92-95	96-99	100-103	104-107	108-111	112-115	116-119	120-124	Ave.[3]	Mean[3] Dev.	Hybrid Index
Mylocheilus	1	9	5	5	....	....	....	....	....	95.9	2.9	
Hybrids	....	....	....	11	8	1	....	....	....	103.8	2.0	45
Ptychocheilus	....	....	....	....	1	6	8	3	2	113.4	3.0	

[3] The averages and the mean deviations were computed from the uncombined data.

Scales.—The number of scales in the lateral line of the chub and squawfish cannot be used for the separation of individuals, because of the wide overlap. *Mylocheilus*, however, has a slightly higher average. On the average, the hybrids fit in between the parental types (hybrid index, 67). A better scale count index is the number of scales above the lateral line. In the chubs, the scales are larger and less crowded before and below the dorsal fin than they are in the squawfish. The hybrids have an index of 43 in this count. In the count of scales below the lateral line, the chubs have a lower average than the squawfish, and the hybrids, for some reason that is not obvious, have a higher average than either of the parental species (the index, not very trustworthy, is 267) (table 4).

There are no marked differences between the parental species in the shape of the scales or in the position of scale radii. There appears to be an average difference, though variable, in the number of radii that reach the scale margin. The scales selected for study were those in the row above the lateral line, directly over the insertion of the pelvic fin. In the *Mylocheilus*, the number of radii varies from 5 to 11, with an average of 7.5.

TABLE 4.—Frequency distribution of scales in the lateral line, scales above the lateral line, and scales below the lateral line of hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense*, and of the parental species

Scales in lateral line	68	69	70	71	72	73	74	75	76	77	78	Ave.	Hybrid Index
Mylocheilus	1	....	....	2	1	1	5	2	4	2	2	74.4	
Hybrids	1	....	2	2	2	3	5	1	1	3	....	73.2	67
Ptychocheilus	1	....	3	3	3	2	3	2	3	....	....	72.6	
Scales above lateral line	13	14	15	16	17	18							
Mylocheilus	3	15	2	....	....	....						13.9	
Hybrids	....	6	10	4	....	....						14.9	43
Ptychocheilus	....	1	3	7	8	1						16.2	
Scales below lateral line	9	10	11	12	13								
Mylocheilus	4	15	1	....	....							9.8	
Hybrids	1	....	9	9	1							11.4	267
Ptychocheilus	2	11	5	1	1							10.4	

Ptychocheilus has a range from 8 to 23 and averages 11.1. The number of radii on the scales of the hybrids ranges from 7 to 19, averaging 11.5. The corresponding index (111) is not very reliable, due to the great fluctuations in counts.

Dorsal and anal rays.—Each hybrid and each of the parental forms has 8 rays in the anal fin. In the dorsal fin, however, the chubs generally have 8 rays and the squawfish 9. The hybrids approach the chubs in this count. The index is 10 (table 5).

TABLE 5.—Frequency distribution of rays in the dorsal fin of hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense, and* of the parental species

	8	9	10	Average	Hybrid Index
Mylocheilus	20	....	....	8.0	
Hybrids	18	2	....	8.1	10
Ptychocheilus	....	18	2	9.1	

Pharyngeal teeth.—One of the most trenchant differences between *Ptychocheilus* and *Mylocheilus* is in the form of the pharyngeal teeth and arch. The chubs have blunt, grinding teeth implanted on a heavier arch and usually arranged according to the formula 1, 5-5, 1. The squawfish have sharp, hooked teeth, generally with the formula 2, 5-4, 2. In form, the pharyngeal teeth of the hybrids closely resemble those of the squawfish, as they are fairly sharp and slightly hooked. In counts (table 6), however, they are in

TABLE 6.—Frequencies of pharyngeal-tooth formulae in hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense,* and in the parental species. Missing teeth, ascertained by the alveoli and by the spacing, were included in the counts. The count of teeth on the left arch is listed first.

Tooth Formula	*Mylocheilus*	Hybrids	*Ptychocheilus*
0, 3-4, 0	....	1	....
2, 4-4, 1	....	1	....
1, 4-5, 0	2	....	....
1, 4-5, 1	6	....	....
2, 4-5, 2	....	1	....
1, 5-4, 1	1	1	....
1, 5-4, 2	....	....	2
2, 5-4, 1	....	1	3
2, 5-4, 2	....	2	13
1, 5-5, 0	1	....	....
1, 5-5, 1	36	7	1
1, 5-5, 2	....	2	....
2, 5-5, 2	....	4	1
1, 5-6, 1	1	....	....

general intermediate (table 7). The total count is almost precisely interjacent (index, 54) and this intermediacy holds for each section and for each tally, with two exceptions: (1) the average for the teeth of the main row of the left side in the hybrid is displaced downward by the one count of only 3 teeth (an abnormal number); (2) the total count for the right arch

TABLE 7.—Mean number of teeth on the pharyngeal arches in hybrids between *Mylocheilus caurium* and *Ptychocheilus oregonense*, and in the parental species. Based on data in table 6

	Mylocheilus	Hybrids	*Ptychocheilus*	Hybrid Index
Main row, left arch	4.83	4.80	5.00	−18
right arch	5.00	4.70	4.10	33
total	9.83	9.50	9.10	45
Lesser row, left arch	1.00	1.40	1.85	47
right arch	0.94	1.40	1.80	53
total	1.94	2.80	3.65	50
Both rows, left arch	5.83	6.20	6.85	36
right arch	5.94	6.10	5.90	400
grand total	11.77	12.30	12.75	54

in the hybrid averages higher than in either parental species, due to a closer approach to the *Mylocheilus* in the number of teeth in the main row on that side, which is typically 5 in that genus and 4 in *Ptychocheilus*. The variants in the *Mylocheilus*, oddly, usually have a higher count on the right side than on the left, which is contrary to the situation in the *Ptychocheilus* and in most cyprinids having bilateral asymmetry in the number of pharyngeal teeth (Hubbs and Hubbs, 1945). There is a greater variability in the tooth formulae of the hybrids than in either of the parental species. This was also true of hybrids between *Gila* and *Siphateles*, as reported by Hubbs and Miller (1943). None, however, had such an abnormal number as did a hybrid between *Acrocheilus aleutacum* and *Ptychocheilus oregonense* described by Hubbs and Shultz (1931).

Color.—The colors in the following descriptions were noted from specimens freshly preserved in formalin. Most of these specimens were taken during or near their spawning season, when the hues are brighter than at other times. The general color of *Ptychocheilus* is dark olive over the back and sides of the body and on the top of the head. The belly and throat is pearl with a tinge of yellow. Although they have much the same background coloration, the chubs have localized areas of brilliant red, which render them among the brightest minnows in the West. There is a blotch of red at the angles of the jaw, and this color continues in a stripe along the cheek below the eye to the origin of the pectoral fin, and, in varying intensity, along the sides of the body. Red is entirely lacking on the squawfish. Also, the chubs have two obvious dark stripes along the sides. The ventral one extends from the end of the operculum posteriorly in a narrownig band to above the origin of the anal. The second stripe starts at the upper half of the operculum and runs along the side above the lateral line to the dorsal fin, where it expands ventrally to include the lateral line. It extends to the base of the caudal. The dorsal dark band is separated from the dark of the back by a narrow pale line.

The hybrids have a more splotchy appearance than either the chubs or the squawfish, but, in general, they are intermediate in color. Thirteen have no red pigment about the mouth, but 3 have obvious red around the angles of the jaw, and 4 others have in this region xanthophores that are discernible under magnification. None has red on other parts of the body. All have

two dark bands down their sides like the chub, but the bands are broken and less distinct.

Chubs have no pigment on the tip of the lower jaw, but squawfish have a small patch of melanophores in this position. Seventeen of the 20 hybrids have a slight scattering of melanophores on the tip of the lower jaw.

Sex ratio and condition of gonads.—A microscopic examination of teased pieces of the gonads showed that the hybrids represent both sexes. Fifteen are males, and of these, 7 are either immature or spawned out, and 8 have large and apparently ripe testes. Of the five females, 4 have small ovaries containing minute eggs of various sizes, and one has large ovaries filled with ova about as large as those in ripe chubs. From this gross gonadal examination, there is no indication that the hybrids are sterile.

The observed ratio of three males to one female suggests that males predominate in this cross, as indicated for hybrid sunfish (Hubbs and Hubbs, 1933; Bailey and Lagler, 1938). Too few of the *M. caurinum* × *P. oregonense* specimens were available, however, to warrant drawing a definite conclusion, particularly since the sexes of fishes often come into a spawning area in disproportionate ratios. From July 5-15, 1951, a total of 57 females and 94 males of *Mylocheilus* were netted in Flathead Lake, and from June 6 to July 15, 43 females and 20 males of *Ptychocheilus*.

YEARLINGS FROM FLATHEAD LAKE

In an unusual seine haul in Yellow Bay of Flathead Lake on July 8, 1950, Dr. Reeve M. Bailey took 37 specimens of *Mylocheilus caurinum* × *Ptychocheilus oregonense* along with 25 of *M. caurinum* and 130 of *P. oregonense*. All were yearlings. Dr. Bailey kindly loaned the hybrids (UMMZ 161874) for a study to be included in this report. Such evidence of mass hybridization of fishes in nature has seldom been noted. Hubbs and Miller (1943) found swarms of hybrids between *Gila* and *Siphateles* in the Mohave Desert, but this had evidently been unnaturally induced by the introduction of an exotic stream species into waters containing a single native minnow maladjusted to stream life (Hubbs and Hubbs, 1947).

Comparison of yearling hybrids with yearlings of M. caurinum and P. oregonense.—The most striking differences in proportions between yearling chubs and squawfish are, as in the adults, the relative size of the head and jaw and the position of the dorsal fin. There are also distinctions in the distribution of melanophores. The presence or absence of barbels on the young hybrids could not be accurately determined, and the scale and pharyngeal teeth counts were not made, because of the small size of the specimens. The comparisons (table 8) involved 35 hybrids, 6 chubs, and 20 squawfish, all yearlings from Flathead Lake. Two hybrids were not included in the calculations as they were warped in preservation.

In the yearling chubs, the upper jaw reaches only as far back as the nasal septum, whereas in the yearling squawfish it reaches to below the anterior margin of the pupil. In the intermediate hybrids, the jaw reaches to below a point between the anterior margin of the orbit and the posterior nasal opening. The hybrid index for the number of times the jaw length goes into the head length is 43 (table 8), as compared with 54 for the adult

TABLE 8.—Proportional measurements of yearling hybrids between *Mylocheilus caurinum* and *Ptychocheilus oregonense*, and of the parental species

	Mylocheilus	Hybrids		*Ptychocheilus*
Year of collection and number of specimens	1950 (6)	1950 (35)	1951 (6)	1950 (20)
Standard length, mm				
Range	44-55	38-65	37-48	32-56
Average	51.1	43.4	42.2	42.1
Standard length / Head length				
Range	3.66-3.94	3.23-3.61	3.33-3.56	3.16-3.42
Average	3.84	3.42	3.44	3.28
Mean deviation	0.10	0.07	0.07	0.05
Hybrid index	....	75	72	....
Head length / Upper jaw length				
Range	3.42-3.75	3.10-3.60	3.11-3.52	2.60-3.33
Average	3.59	3.30	3.33	2.91
Mean deviation	0.12	0.11	0.12	0.14
Hybrid index	....	43	38	....
Index, dorsal fin position[4]				
Range	100-107	102-115	106-110	113-125
Average	101	108	108	118
Mean deviation	3.00	2.20	1.33	2.70
Hybrid index	....	41	41	....

[4] Distance from dorsal origin to tip of snout, times 100, divided by distance from dorsal origin to end of scales on base of caudal fin.

hybrids. In relative head length, the hybrid index is 75 (49 for adults), but in position of the dorsal fin, the hybrids are more nearly intermediate, with an index of 41 (45 for adults). All fishes, both hybrids and parental species, have 8 rays in the anal fin, with the exception of 1 squawfish which has 9. All the *Mylocheilus* specimens have 8 dorsal rays; 19 specimens of *Ptychocheilus* have 9 dorsal rays and 1 has 10 rays; and of the hybrids, 31 have 8 dorsal rays and 4 have 9. The hybrid index is 10, as in the adults. The low ray count is probably dominant.

Juvenile squawfish have a well-defined basicaudal black spot, which disappears in the adults. Young chubs lack this marking. In all but two of the hybrids, a dark blotch is readily distinguishable at the base of the caudal, but in none is it as well defined as in *Ptychocheilus*. The chubs have no dark chromatophores on the lower jaw and have only a few dispersed ones on the upper, whereas the squawfish have obvious melanophores on the tip of the lower and upper jaw. On both jaws of the hybrids there is a scattering of melanophores which are not nearly as crowded as on the squawfish yearlings. In other color characters, the three groups of fishes are similar. They have a narrow dark stripe the length of the back, and a dusky band from the caudal base to below the origin of the dorsal.

Six additional yearlings of this hybrid were seined from the shallows of Yellow Bay, Flathead Lake, in the summer of 1951. Included in the same lot were 13 specimens of *Mylocheilus caurinum*, 30 of *Ptychocheilus oregonense*, and 75 of *Richardsonius balteatus*. There were no other data

with these specimens. The measurements on these hybrids are also given in table 8. The hybrid indices, based on the values for the parental species of the 1950 collection, are almost identical with those of the other hybrids. In pigmentation they also agree. Of the six specimens, four have 8 dorsal rays and two have 9 (hybrid index, 31). All have 8 anal rays.

PTYCHOCHEILUS OREGONENSE × RICHARDSONIUS BALTEATUS

Two hybrids of the cross between the squawfish and the redside shiner were seined on March 20, and another one on April 8, 1950, from a warm spring slough on the north side of Highway 10, about two miles east of Bearmouth, Montana. The waters from this slough feed directly into the Clark Fork River. Also taken on these two days were 219 squawfish

TABLE 9.—Counts and proportional measurements of hybrids between *Ptychocheilus oregonense* and *Richardsonius balteatus*, and of their parental species

	Ptychocheilus	Hybrids	*Richardsonius*	Hybrid Index
Standard length, mm				
Range	101-166	124-140	59-66	
Average	135	132	62	....
Scales in lateral line				
Range	71-73	61-67	52-55	
Average	72	65	54	61
Rays in dorsal fin				
Range	8-9	9-11	9-10	
Average	8.75	9.33	9.75	42
Rays in anal fin				
Range	8	10	14-15	
Average	8	10	14.2	68
Pharyngeal teeth	2, 5-4, 2	2, 5-4, 2	2, 5-4, 2	....
Supraorbital pores				
Range	16-17	12-14	8-10	
Average	16.75	13.33	8.75	57
Standard length / Head length				
Range	3.5-3.7	3.5-3.8	3.7-4.0	
Average	3.65	3.63	3.89	108
Standard length / Greatest depth				
Range	4.5-4.8	4.2-4.3	3.3-3.5	
Average	4.60	4.23	3.42	69
Head length / Snout length				
Range	2.9-3.1	3.1-3.3	3.5-3.9	
Average	3.03	3.19	3.65	74
Head length / Eye width				
Range	5.3-5.8	4.7-5.1	3.4-3.8	
Average	5.5	4.9	3.5	70

and 169 redside shiners. Milt flowed easily from adults of these fish. Besides the putative parents, associated species included *Catostomus catostomus, C. macrocheilus,* and *Salmo trutta.*

Adults and juveniles of the two parental species are easily differentiated. The large eye, deep body, brilliant colors, fewer lateral line scales, and especially the large number of rays in the anal fin of the *Richardsonius* distinguish it from the *Ptychocheilus.* In this part of Montana the squawfish may reach a length of over 75 cm, whereas the largest shiner we have recorded is 13.3 cm in total length.

The four specimens of each parental type that are compared with the three hybrids in table 9 were taken in the same net hauls as the hybrids.

Considering the few specimens collated and the discrepancy in size between the examples of the parental species, it is noteworthy that the hybrids appear to be intermediate in all characters studied except relative head length. They are also intermediate in characters other than those listed in the table. The scarcely oblique and nonangulate mouth of the squawfish contrasts with the angulate upper jaw and oblique mouth of the shiners; the hybrids have a slightly angulate upper jaw and the mouth is more oblique than that of the squawfish. The distance from the origin of the dorsal fin to the end of the scales on the caudal base when measured forward extends in the squawfish to some point between the middle of the pupil and the nostril; in shiners, only to a point between the posterior margin of the orbit and the upper angle of the gill cleft; in the hybrids, to the upper end of the preopercle.

The hybrids resemble the squawfish in color, except in that they are somewhat lighter and have blotches and specks of black against the olive of the back and sides. Completely lacking are the brilliant red and brassy sheens that render the redside shiner one of the most beautiful of North American cyprinids. This lack was noted even on a freshly caught specimen, before it was preserved.

RHINICHTHYS CATARACTAE × RICHARDSONIUS BALTEATUS

The crosses between the redside shiner and the longnose dace were seined from the mouth of an irrigation ditch that flows into Post Creek, a tributary of Flathead River. Four hybrids were collected on March 26 and May 20, 1950, along with 7 dace, 719 shiners, and juveniles of *Ptychocheilus oregonense* and *Catostomus macrocheilus.* In May, male dace and shiners could be stripped.

A fifth specimen of the same hybrid combination was taken on December 11, 1951, from an irrigation ditch about 5 miles west of Missoula on the old Frenchtown road. Included in this collection were 2 dace, 320 shiners, a large series of *Catostomus catostomus, C. macrocheilus, Ptychocheilus oregonense,* and a few specimens of *Cottus cognatus.*

The hybrids do not approach exact intermediacy in any of the characters treated in table 10, but their measurements do fall between the

TABLE 10.—Counts and proportional measurements of hybrids between *Rhinichthys cataractae* and *Richardsonius balteatus*, and of their parental species. Based on all 5 hybrids (4 from the Post Creek ditch) and on 4 specimens from the Post Creek ditch of each parental species.

	Rhinichthys	Hybrids	*Richardsonius*	Hybrid Index
Standard length, mm				
Range	39.0-56.0	38.0-50.0	51.0-78.5	
Average	46.0	43.1	66.1	....
Scales in lateral line				
Range	59-68	56-63	54-59	65
Average	64.0	58.8	56.0	
Rays in dorsal fin				
Range	8	8-9	9-11	
Average	8	8.8	10.0	40
Rays in anal fin				
Range	7	8-10	15-16	
Average	7	9.2	15.3	27
Pharyngeal teeth	2, 4-4, 2	2, 5-4, 2	2, 5-4, 2	....
Standard length / Head length				
Range	3.4-3.7	3.7-3.9	3.7-3.9	
Average	3.5	3.8	3.8	100
Head length / Snout length				
Range	2.2-2.5	2.4-2.9	3.2-3.9	
Average	2.3	2.7	3.5	33
Head length / Eye width				
Range	4.3-5.7	3.6-4.0	3.2-3.6	
Average	4.9	3.8	3.4	74
Standard length / Greatest depth				
Range	4.8-5.6	4.6-5.2	3.6-3.9	
Average	5.3	4.9	3.7	25

averages for those of the very distinct parental species. The putative parents differ in other marked respects, in all of which the hybrids are interjacent. The longnose dace have a ventral and horizontal mouth overhung by the snout and reaching to below the middle of the nares. The mouth of the shiners is terminal, somewhat oblique, not overhung by the snout, and reaches to below the anterior margin of the orbit. In the hybrids, the intermediate mouth is slightly oblique and is scarcely overhung by the snout, and reaches to below the posterior margin of the nares. All of the dace have a barbel in each jaw angle. This is lacking in the shiners. Four of the hybrids are without barbels, but one has a rudimentary barbel on the right side only. All specimens of the *Rhinichthys* have a well-developed frenum, which is not evident on the *Richardsonius*. Three hybrids have slightly developed frenums, one has a well-developed frenum, and one has none.

The dorsal fin is more anterior on the dace than on the shiners. The distance from the origin of the dorsal to the last caudal scales when measured forward extends in the dace to the tip of the snout or to the anterior nares; in the shiners, to the upper angle of the gill opening; in the hybrids, to the anterior margin of the orbit. The internarial flap is exceptionally large in the *Rhinichthys;* much smaller in the *Richardsonius;* and of intermediate size in the hybrids.

The colors of all of the fishes taken from the Post Creek ditch were atypical. The water in the ditch is the color of skimmed milk, derived from the clay beds over which it flows. The fishes had assumed a remarkably white color in this water. It can be noticed, however, that the hybrids resemble the *Rhinichthys* and differ from the *Richardsonius* in lacking melanophores on the lower jaw, and that they have, like *Richardsonius*, a definite black stripe along the back. The hybrid that came from the ditch west of Missoula is much darker. Although it lacks the narrow black stripe down the mid-dorsal line, it has a broad, broken band of black from the operculum to the caudal base and dark mottlings over the back.

SUMMARY AND CONCLUSIONS

The validity of using intermediate characters to distinguish fish hybrids has been amply discussed by Hubbs, Hubbs, and Johnson (1943). Furthermore, centrarchid hybrids reared experimentally in the laboratory support the contention that they can be identified by such methods (Hubbs and Hubbs, 1932, 1933). Although the evidence is purely circumstantial, there is little doubt that the specimens under discussion from western Montana are naturally occurring hybrids of the combinations *Mylocheilus caurinum* × *Ptychocheilus oregonense, Ptychocheilus oregonense* × *Richardsonius balteatus,* and *Rhinichthys cataractae* × *Richardsonius balteatus.* These fish meet the test of being intermediate in most of the characters of their putative parents. The grand average of the hybrid indices mentioned in the text for *M. caurinum* × *P. oregonense* adults (using for the pharyngeal teeth only the index derived from the total count on both sides) is 78, but it is 46 if the doubtful differentiating characters of scales below the lateral line and the number of radii on the scales are omitted. For two sets of yearlings of this same cross, on the basis of fewer characters, the overall indices are 42 and 45, respectively. For *P. oregonense* × *R. balteatus,* the grand average hybrid index is high (69), and for *R. cataractae* × *R. balteatus* it is 52, very close to exact intermediacy. Thus, the traits as a whole are intermediate. Despite the obvious crudity of the procedure, it is considered more definitive to show the relationship with the average of the various hybrid indices rather than only with the indices of single characters. This grand average expresses traits as a whole and minimizes isolated characters that tend to resemble one parent more than the other or are extremes in hybrids. It is true, however, that the inclusion or exclusion of just one character that veers radically from intermediacy can alter the grand average considerably.

Also in support of the identification made of these fishes is the circumstance that certain basic conditions required for hybridization are met. The species assumed to miscegenate were present in the same water, and

observations intimate no barrier to choice of spawning grounds or in time of breeding. In each combination, mature males of the parental types could be stripped of milt, indicating that their breeding seasons are concurrent.

A number of factors have been suggested as conducive to hybridization. Among these are crowding of spawning fishes, the cohabitation of a rare and an abundant species, and the introduction of an exotic species (Hubbs, Walker, and Johnson, 1943; Hubbs and Hubbs, 1947).

The ecological basis for hybridization between *P. oregonense* and *M. caurinum* is possibly the results of the crowding of spawning fishes, recently caused by a man-made hydrographical change. The water in Flathead Lake, where the hybrids were captured, has been maintained at a considerably higher spring and summer level after Kerr Dam was built at its outlet in 1938. Old-timers around the lake claim that much of the sloping gravel shore line, which formerly undoubtedly served as the spawning grounds for squawfish and chubs, is now inundated in these seasons to a considerable depth. Most of the large margin at present is composed of mud or precipitous rocky banks. With the reduction in good breeding sites, the two genera are limited to reproducing in areas small for the numbers of fish which the large lake can otherwise support. This factor should be inspected by wildlife managers, as in time such situations may affect considerably the fish population of the Northwest, where dam construction is proceeding at a rapid pace. Incidentally, no hybrids were taken in other lakes where we have made large collections including both Columbia River chubs and squawfish. These lakes have relatively long shallow shore lines of sand and gravel.

At the time the *Ptychocheilus oregonense* × *Richardsonius balteatus* combinations were taken, we had been studying the breeding habits of the redside shiner, and noticed that a few squawfish swam into the welling spring waters where the shiners were spawning, whether to spawn themselves or to feed on shiner eggs we could not determine. In several respects, the warm spring slough in which these studies were made is ideal for hybridization. Its banks are mud, and the only places suitable for spawning are restricted to the gravel mouths of several warm springs along its shore line. It is extremely rich in fish food and supports a remarkably large population of squawfish and shiners. Frequent observations evince that most of the fish inhabit the slough for the entire year, but that during the spawning season others crowd in through its outlet from Clark Fork River. The encroachment by river fishes is probably intensified by changes man has wrought on the environment. Clark Fork River is somewhat polluted by wastes, from the copper smelter at Anaconda, which make its backwaters less desirable for spawning. Also, many of its pure feeder streams are blocked to fish passage by flumes and viaducts. The combination of large breeding populations of both species, and the confined spawning grounds certainly promotes hybridization.

The warmth of the slough water, which remains fairly constant at 17-18° C, may also be a factor conductive to miscegenation between the squawfish and the shiner. We have noticed in typical streams and lakes of western Montana that the shiners ripen several weeks to a month earlier than the squawfish. The warm waters may cause the two species to ripen at approximately the same time.

Crowding of breeding fishes cannot be an explanation for the reported crossing of *Rhinichthys cataractae* with *Richardsonius balteatus*, for the place where they were captured affords ample spawning grounds. Hybridization in this case may be enhanced by the fact that the dace is rare in the stream, whereas the shiners are extremely abundant, a case analagous to that which Hubbs, Hubbs, and Johnson (1943) found for some sucker hybrids, and that Hubbs, Walker, and Johnson (1943) found for certain cyprinodont hybrids. Perhaps another, but less plausible, factor contributing to this cross is the murky condition of the water and the similarity in colors of the different fish species. If sexual selection in these minnows is based at least in part on coloration, a normal barrier to crossing would not be effective in this environment. However, we obtained one *R. cataractae* × *R. balteatus* hybrid in another ditch where the water was fairly clear.

Particular ecological conditions seem to be much more potent than random chance in determining whether cohabitants, which are genetically compatible and which utilize similar spawning areas at the same season, hybridize in nature. In the last three years, extensive collections from many different streams and lakes containing the same species of fishes have revealed that hybrids are to be found only in certain localities. In Flathead Lake, the chub-squawfish combination has been taken on nine different occasions over a period of two years, and it has not been taken elsewhere. The factors that seem to lead to miscegenation and to the production of partially fertile or infertile hybrids should be considered seriously in fish management, at least until they are proved to be invalid.

At the present time, there are few indications that these particular hybrids backcross with their progenitors. It is true that they were collected with their parental types during the spawning season, and that some of the gonads from *M. caurinum* × *P. oregonense* appeared on gross examination to be normal and ripe. However, we have not identified any fish as intermediate in characters between a hybrid and one or the other of its parental species. Since all species involved in these crosses are native, sufficient time has been provided for the admixture of genes if the hybrids were fertile and if they were to interbreed or backcross freely. From the available data, it would seem that the proportion of hybrids to their parental kinds is large enough to greatly affect the genetic constitution of the population, if those conditions should have been met. It must be assumed that the hybrids do not reproduce at all extensively.

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Two New Genera of Hydracarina from a Spring in Northern Michigan[1]

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During the summers of 1951 and 1952, collections were made in a small spring in the vicinity of the University of Michigan Biological Station. The spring is of the rheocrene type and, except when ground runoff was high, the temperature remained very close to 10.5°C during the time it was studied. The bottom is largely sand, with occasional areas of muddy sand and sandy mud. The dominant vegetation was *Nasturtium officinale* R. Br. This situation is extremely rich in water mites. In addition to the two hydrachnids described in this paper, representatives of the genera *Hydrovolzia, Thyas, Panisus, Panisoides, Sperchon, Lebertia, Hygrobates, Megapus, Pseudofeltria,* and *Aturus* were taken. Most of these species still await description. Adult mites were most abundant in June and early July with the immature stages becoming more numerous around the middle of the latter month.

Hydryphantidae
Subfamily Thyasinae

Thyopsella n. gen.

Figs. 1-9

Generic diagnosis.—Large, reticulate dorsal shield present; lateral eyes in capsules; unpigmented median eye surrounded by a plate made up of the fused prefrontalia, postfrontalia, dorsocentralia 1 and dorsolateralia 1; dorsocentralia 2 and 4 fused with their respective dorsolateralia; dorsocentralia 3 separated from dorsolateralia 3 in nymphs and newly metamorphosed adults, but appearing fused in older adults; dorsocentralia 5 fused to form a large plate at the posterior end; three pairs of elliptical genital acetabula present, second pair midway between the first and third pairs; dorsoglandularia 2-7 lying in clear spaces in the integument; chelicerae similar to those found in *Thyas.*

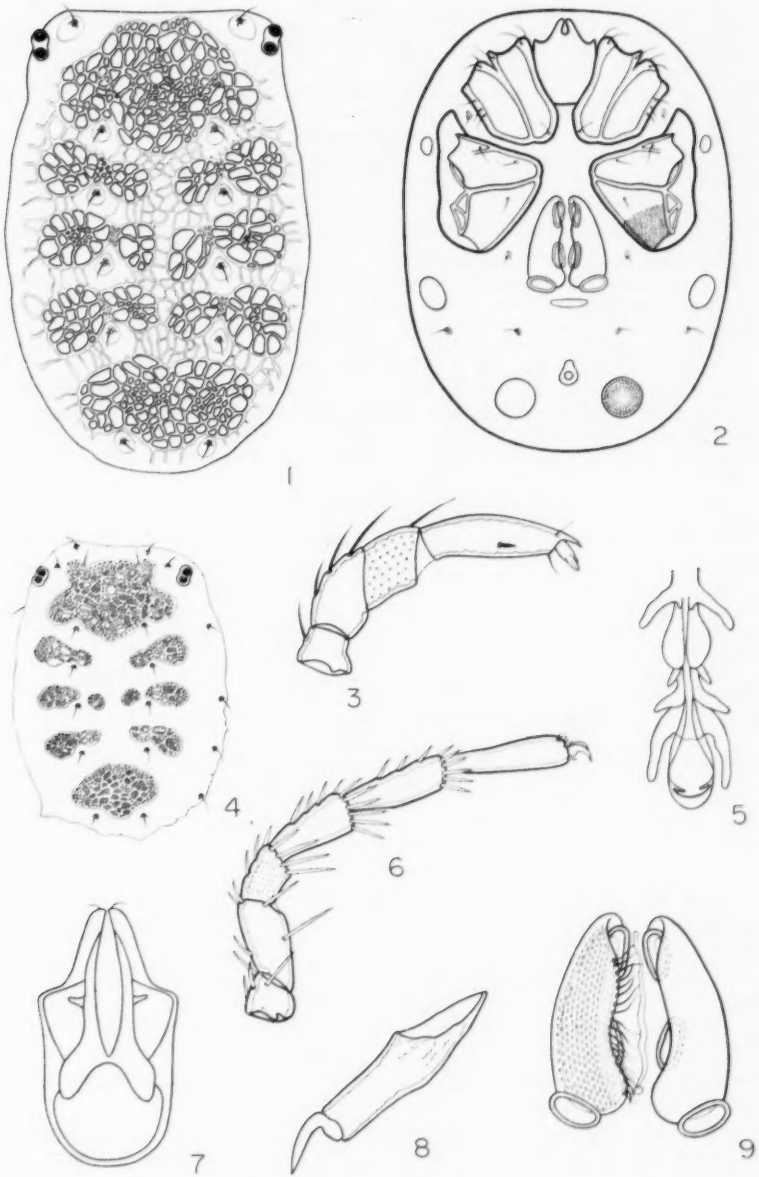
Genotype.—Thyopsella dictyophora n. sp.

Thyopsella differs from all other Thyasinae which bear a complete dorsal shield by possession of the following characters: 1) The dorsal plates make up only about one-half of the total area of the dorsal shield; 2) Dorsocentralia 2 and 4 fused to their respective dorsolateralia.

Thyopsella dictyophora n. sp.

Male.—Length of dorsal shield 0.86-1.18 mm, width of dorsal shield 0.59-0.77 mm. Dorsal shield elliptical, truncate at anterior end; median eye without pigment; frontal plate composed of the fused pre- and postfrontalia, dorsocentralia 1 and the dorsolateralia

1 Contribution from the Department of Zoology, University of Michigan and the University of Michigan Biological Station. This paper represents a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author wishes to express his sincere appreciation to Dr. Frank E. Eggleton for his helpful advice during the course of this study, and to Dr. Alfred H. Stockard for making available many of the facilities of the University of Michigan Biological Station.



Figs. 1-9. *Thyopsella dictyophora.*—1. Dorsal shield of male; 2. Ventral view of male; 3. Inner side of left palp, male; 4. Dorsal view of nymph; 5. penis; 6. Second leg, left side, male; 7. Dorsal view of capitulum; 8. Chelicera; 9. Genital field, male.

1; frontal plate appearing four-lobed; postocularia also lying on this plate; dorsocentralia 2 and 4 fused with their respective dorsolateralia, somewhat constricted at point of fusion; dorsocentralia 3 appearing fused in older males, but slightly separated in newly metamorphosed individuals; dorsolateralia slightly larger than dorsocentralia; dorsocentralia 5 fused to form a larger somewhat three-lobed plate at the posterior end; dorsoglandularia 2 located slightly anteriorad and mesiad to the eyes, other dorsoglandularia placed just posterior to the point of fusion of the dorsocentralia and dorsolateralia; dorsoglandularia surrounded by oval, clear spaces in the integument; plates and integument of the dorsal surface broken up by reticulations (reticulations often much finer than that shown in fig. 1); ventral surface soft; ventralia 2 round or elliptical, 0.068-0.108 mm in diameter; postgenitale much wider than long, located just posterior to the genital flaps; genital acetabula elliptical, first and second pairs covered by genital flaps when the latter are closed; third pair of genital acetabula lying at posterior end of the genital flaps, long axis of these acetabula at right angles to the long axis of the body; second pair of genital acetabula located midway between first and third pairs; genital flaps 0.20-0.23 mm in length, 17-21 setae present along the inner margin of each side.

Legs without swimming hairs, similar to those of *Thyas;* fig. 6 shows arrangement of setae on the second leg; capitulum 0.21-0.24 mm in length, rostrum moderately developed; penis 0.21-0.24 mm in length; palp with a stout bristle on inner side of P-IV, this bristle approximately midway between the two ends. The dorsal lengths of the palpal segments, in millimeters, based on five randomly picked specimens are: P-I, 0.040-0.042 mm; P-II, 0.090-0.096 mm; P-III, 0.050-0.060 mm; P-IV, 0.160-0.174 mm; P-V, 0.036-0.044 mm.

Female.—Length of dorsal shield 1.19-1.33 mm; width of dorsal shield 0.77-0.86 mm; length of capitulum 0.24-0.26 mm; length of genital flaps 0.24-0.25 mm.

Female similar to male except that it averages larger and the dorsal shield is usually more reticulate.

Nymph.—Dorsal plates similar to those of adult except that dorsocentralia 3 and dorsolateralia 3 are widely separated from each other; frontal plate lobed near anterior corners, lobes forming bays, each of which enclose a seta; integument of dorsum not reticulate; provisional genital field with two pairs of genital acetabula.

Holotype.—Adult male, taken in a spring at the base of Maple River Dam, Emmet Co., Michigan (T36N/R4W/S10) on June 17, 1952.

Allotype.—Adult female, same date and locality as holotype.

Nymphotype.—Taken in same locality on August 22, 1951.

All three major types will be deposited in the Chicago Natural History Museum.

Paratypes.—Seventeen males, twelve females, same locality as the holotype, between June 23, 1951 and July 15, 1951. Thirty-one males, twenty-five females, one nymph, same locality between June 17, 1952 and June 26, 1952.

Range.—Known only from the type locality.

The systematic position of *Thyopsella* among the other thyasid genera is uncertain. At the present time there are only four other genera belonging to the Hydryphantidae which possess dorsal shields. Three of these, *Teratothyas* Viets 1929, *Teratothyasides* Lundblad 1941, and *Hansvietsia* Viets 1951, represent very divergent offshoots from the main thyasid line and have been placed in the subfamily Teratothyasinae. This latter subfamily differs from the Thyasinae in the following respects: The median eye is poorly developed or missing; the dorso- and lateroglandularia lie on the dorsal plates; the palps are not chelate; and the chelicerae are stilet-like.

The only other genus in the subfamily Thyasinae with a dorsal shield is *Thyopsis* Piersig 1898. In *Thyopsis* the dorsal shield is composed largely of the dorsal plates and the nymph possesses a dorsal shield similar to that of the adult. In *Thyopsella* the area occupied by the dorsal plates is not as extensive and the nymph lacks a dorsal shield. The differences between the nymphs of *Thyopsis* and *Thyopsella* would suggest that they are not closely related

genera. The nymph of *Thyopsella* resembles a *Panisus*-like form in which the dorsolateralia have fused to the dorsocentralia. Since only the adult of *Thyopsella* possesses a dorsal shield, it may well be a character which has arisen rather late and is of little phylogenetic value.

ARRENURIDAE

Subfamily **Laversiinae** n. subfam.

The combination of the following characters place *Laversia* distinctly apart from the rest of the Arrenuridae, and necessitates the establishment of a new subfamily adequately to receive it. The subfamily Laversiinae is characterized as having: Glands E-1 placed near the middle of the second epimera instead of between the second and third pairs; posterior end of the capitulum greatly lengthened in contrast to the rest of the Arrenuridae; genital field of the male modified from that characteristic of the family. The following characters are not confined to *Laversia*, but are found in only one other genus or subgenus of the Arrenuridae: Palps not uncate, antagonistic bristle missing (this is also the case in the subgenus *Micruracaropsis* of the genus *Arrenurus*); no development of a cauda in the male, which is also true in the genus *Africasia* Viets.

Laversia n. gen.

Figs. 10-18

Generic diagnosis.—Dorsal and ventral shields present; dorsal furrow complete; swimming hairs absent; distal end of P-IV not expanded, not forming an uncate palp; P-IV without antagonistic bristle; median margin of fourth epimera reduced to a median angle; genital acetabula numerous, located on posterio-laterally directed, wing-like plates; acetabular plates extending between third and fourth epimera in male, between only the fourth in female; I-Leg-6 expanded, similar to that found in *Dadayella clavipes* Lundblad; basal portion of capitulum elongated posteriorly, anterior portion drawn out into a short rostrum; body of male not greatly modified, no development of a cauda; setae-bearing glands of the dorsal shield near periphery; dorsal shield with five pairs of lighter colored, rosette-like areas; glands E-1 located on the second pair of epimera instead of lying in the integument between the second and third pairs; bay formed by the first epimera deep; integumental pores small and closely spaced (approximately 16 in a length of 100 micra).

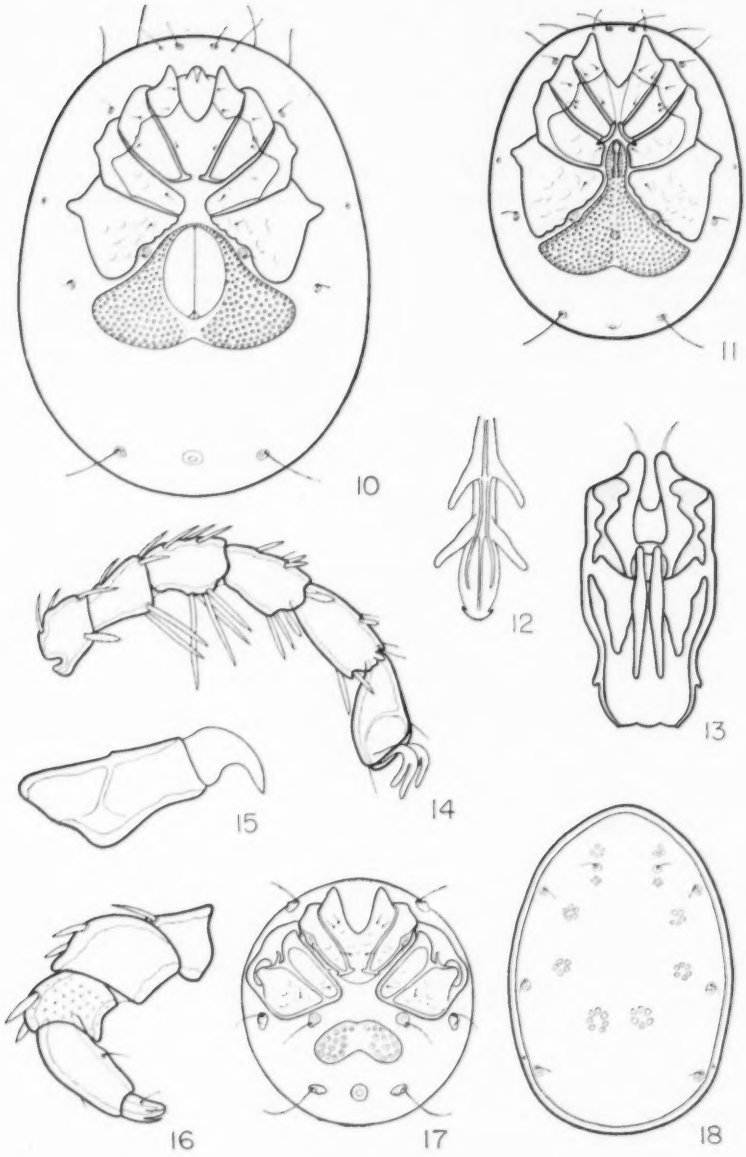
Genotype.—*Laversia berulophila* n. sp.

Laversia seems to be most closely related to the genus *Africasia* Viets 1931. There is no tendency to form a cauda in either genus. The placement of the setae-bearing glands of the dorsal shield is similar in both and from the figures of *Africasia* in Viets' *Sunda Inseln* paper of 1935, it would appear that that genus also has five pairs of rosettes. *Africasia* differs from *Laversia* in possessing an uncate palp, having glands E-1 located between the second and third pairs of epimera, and in the shape of the genital field.

Laversia berulophila n. sp.

Male.—Length of dorsal shield 0.66-0.81 mm, width of dorsal shield 0.47-0.59 mm, length of ventral shield 0.75-0.86 mm, width of ventral shield 0.57-0.64.

Body elliptical; ventral shield widest just below dorsal furrow; dorsal furrow near periphery; dorsal shield flattened; eyes lying just below dorsal furrow, integument forming clear, poreless lenses; dorsal shield with one anterior pair of glandless setae, and three pairs of setae accompanied by glandularia located near the periphery; five pairs of rosette-like areas on dorsal shield; bay formed by first epimera deep; median margin of fourth epimera reduced to a round, median angle; median margin of second epimera with strongly developed apodemes; glands E-1 lying near the center of the second epimera;



Figs. 10-18. *Laversia berulophila*.—10. Ventral view of female; 11. Ventral view of male; 12. Penis; 13. Dorsal view of capitulum female; 14. First leg, left side, male; 15. Chelicera; 16. Inner side of right palp, female; 17. Ventral view of nymph; 18. Dorsal shield of male.

genital field somewhat triangular, extending between the third and fourth pairs of epimera; genital opening between third epimera; acetabular plates elliptical in the area where they surround the genital opening, and gradually spreading posterior to the opening; medial margins of the acetabular plates contiguous; genital acetabula numerous, covering the plates except for a median strip; an irregular number of genital acetabula (two to six) located on either half of the genital opening; glands E-2 located in a slight indentation of the fourth epimera; excretory pore on a slightly raised papilla near posterior end.

Legs without swimming hairs; I-Leg-6 expanded; setae spine-like, those on I-Leg-3 longer than the segment; claws bifurcated; capitulum 0.16-0.17 mm in length, basal portion greatly elongated at posterior end; anterior end drawn out into a short rostrum; setae at anterior end of capitulum rather heavy; penis approximately 0.14 mm in length, similar that found in *Arrenurus;* palps short and stocky; distal end of P-IV not expanded, antagonistic bristle missing; setae of first three segments short and thick, one seta located on P-I, two on P-II, and two on P-III; setae on last two segments hair-like. The dorsal lengths of the palpal segments in millimeters based on five randomly picked specimens are: P-I, 0.040-0.048 mm; P-II, 0.064-0.072 mm; P-III, 0.040-0.044 mm; P-IV, 0.070-0.076 mm; P-V, 0.024-0.028 mm.

Female.—Length of dorsal shield 0.90-1.08 mm width of dorsal shield 0.72-0.79 mm, length of ventral shield 0.99-1.33 mm width of ventral shield 0.76-0.87 mm.

Body similar in shape to that of male; median margin of fourth epimera reduced to a sharp angle; apodemes of median margin of second epimera; not strongly developed; genital field extending between the fourth epimera; genital valves large; acetabular plates short, directed posterio-laterally; genital acetabula numerous; dorsal shield similar to that of male except in size; palps, legs and capitulum similar to male, except that they average slightly larger.

Nymph.—Similar to the nymph of *Arrenurus* except that the palp is not uncate; palp similar to adult except in size; glands E-1 lie on the posterior edge of the second epimera (they lie between the second and third pairs of epimera in *Arrenurus;* acetabular plates of the provisional genital field shorter and more broadly joined at their median borders in *Laversia,* 10-15 acetabular on either side; areas corresponding to the rosettes of the adult dorsal shield present as porous, sclerotized patches on the dorsum.

Holotype.—Adult male, taken in a spring at the base of Maple River Dam, Emmet Co., Michigan (T36N/R4W/S10) on June 17, 1952.

Allotype.—Adult female, same date and locality as holotype.

Nymphotype.—Taken in the same locality on August 22, 1951.

All three major types will be deposited in the Chicago Natural History Museum.

Paratypes.—Twenty-one males, fourteen females same locality between the dates June 23, 1951 and July 15, 1951. One nymph, same locality on August 22, 1951. Twenty-two males, twenty-four females, same locality between June 17, 1952 and June 26, 1952

Range.—Known only from the type locality.

There are seven previously described genera belonging to the family Arrenuridae, all of which have been placed in the single subfamily Arrenurinae. Since males of only four of these seven genera are known, a revision of the family would be of little value at this time. However, on the basis of our present knowledge, two evolutionary tendencies may be seen. One of these trends is toward a strong sexual dimorphism of the body in males (i.e., development of a cauda). In *Arrenurus* this sexual dimorphism varies considerably. Among certain members of the subgenera *Truncaturus* and *Megaluracarus* the cauda is weakly developed, while in the subgenus *Arrenurus* and most species of *Megaluracarus* and *Micruracarus* dimorphism of the sexes is very pronounced. The genera *Rhinophoracarus* and *Thoracophoracarus* appear to be very divergent offshoots from the subgenus *Arrenurus.*

A second group within this family, probably more closely resembling the primitive arrenuroids, is characterized by a lack of a cauda in the males. While

Africasia is the only previously described genus which can be assigned to this latter category, *Laversia* also belongs here. Males of *Dadayella*, *Wuria*, and *Wuriella* are unknown and therefore, the placement of these genera within the Arrenuridae is impossible. If, in the future, mites are found which will link *Laversia* to *Africasia*, it will probably prove desirable to expand the limits of the subfamily Laversiinae to include those arrenuroids without cauda development in the males.

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Seasonal Faunal Variations in a Colorado Alpine Pond[1]

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The peculiar and highly variable physical conditions prevailing in the alpine tundra make it one of the most rigorous of all types of environments. This is true for aquatic as well as terrestrial communities. The fauna of an alpine tundra pond, for example, must be adapted to a very short period of activity when the water is ice-free and to a long period of suspended activity in the frozen bottom of the pond during the winter. It must also be adapted to rapid and extensive daily temperature changes produced by alternating periods of cloudiness, high insolation, cold nights, frequent cold showers, and strong winds.

Although the seasonal hydrobiology of alpine lakes is poorly known, it is further true that even less is known about the hydrobiology of small alpine tundra ponds. The American literature on the ecology of high altitude ponds is exceptionally scanty, most of this information being limited to casual or occasional observations. The European literature is much more extensive, but it is unfortunate that the great majority of such studies are based upon single visits to particular ponds. A few investigations are based upon two, three, or rarely more visits. As a consequence, such publications are necessarily limited to short general discussions, brief descriptions of pond habitats, and lists of species collected during the one or several visits. Typical papers are those of Brink and Wingstrand (1949), Pesta (1933, 1935, 1943), Pichler (1939a, 1939b), Stirnimann (1926), Thomasson (1951, 1952), and Turnowsky (1946).

It therefore follows that our concept of the seasonal appearance, development, and disappearance of animal populations in tundra ponds is exceedingly sketchy, and it is the purpose of the present paper to give a seasonal characterization of a typical Colorado alpine tundra pond based on observations and collections distributed throughout the open season. Emphasis is placed on the seasonal abundance of the major aquatic organisms, exclusive of most of the microscopic forms. The collections were quantitative whenever possible. A few physical and chemical determinations were also made. The study extended from June 29 to October 29, 1950, and this period represents the entire open season of the pond in that year. The data were gathered on 15 trips at seven to 12-day intervals.

The writers are grateful to the National Park Service for permission to make these field collections in Rocky Mountain National Park.

Description of Trail Ridge Pond.—Trail Ridge Pond (hitherto unnamed) is located in Larimer County, Colorado, in the northwestern part of Rocky Mountain National Park at 40° 26′ north latitude and 105° 45′ west longi-

[1] Contribution No. 21, Limnology Laboratory, Department of Biology, University of Colorado.

tude. It may be seen nearly 700 feet below and southwest of Trail Ridge Road from a point about one-quarter mile northwest of the Iceberg Lake parking area (fig. 1). The pond is situated at an elevation of 3507 meters (11,500 feet), approximately at timberline near the head of Forest Canyon. This is well above the 3200 meters suggested by Pennak (1941) as the lower limit of the alpine limnological zone in northern Colorado.

The shape is roughly rectangular with a maximum length of 70 meters and width ranging from 28 to 37 meters (fig. 2). Maximum depth is one meter. Two small marshy sedgegrown islands lie near the southeast corner. The pond basin is saucer-shaped and is not to be confused with the staircase or thrust ponds characterized by Ives (1941).

Geologically, the rock bound basin was formed from rock plucking by a glacierette during late Wisconsin times. The organic fraction of the accumulated bottom deposits can perhaps be best described as a gyttja and förnasapropel combination (Lindeman, 1941). Much of the organic material is coprogenic, but there is also a quantity of macroscopic plant detritus derived from the peripheral sedge growths or blown in from the valley below by frequent strong updrafts. A small amount of sand and bits of angular and flaked siliceous gravel are intermingled with the organic material.

Much of the pond water is derived from surface drainage from the steep talus and tundra slopes to the north and east of the basin. Melting snows contribute much water through the middle or end of July, but thereafter showers and seepage are the chief sources. A broad sluggish outlet is present at the west end. In years when the months of August, September, and October are exceptionally dry, the maximum depth of the pond may fall to only 0.7 or 0.8 meters, but it is essentially a permanent body of water. The summer of 1950 was normal, and the pond maintained its maximum depth of about one meter throughout the period of field work.

Fig. 1.—Trail Ridge Pond as seen from Trail Ridge Road, Rocky Mountain National Park, in midsummer.

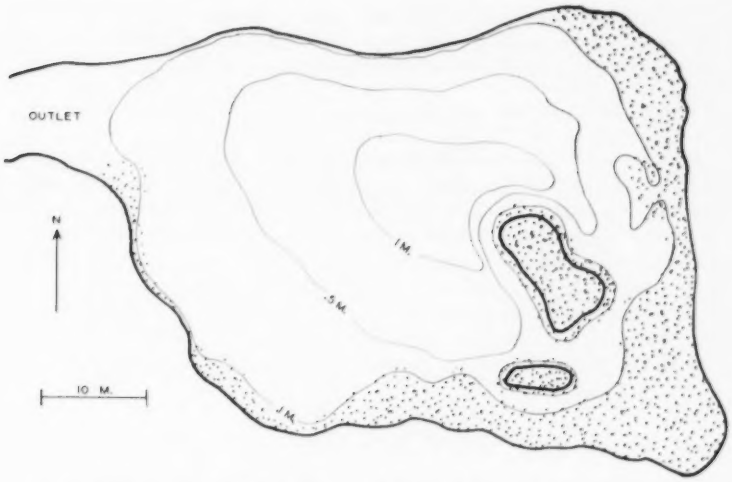

Fig. 2.—Outline map of Trail Ridge Pond. Only the 0.1, 0.5, and 1.0 meter contours are shown. Sedgy area indicated by dots. Note the two small sedgy "islands."

Materials and methods.—The steep and rocky climb between Trail Ridge Pond and Trail Ridge Road made it imperative that lightweight and compact sampling equipment be used. All sampling and measurements were done regularly between 10 a.m. and 3 p.m.

For bottom samples, a small flat-bottomed scoop (12 x 12 x 2.8 cm) was constructed of heavy sheet metal. The total area of bottom sampled with each such scoopful was one-seventieth of a square meter. Five samples were taken on each visit. They were sifted through a number 20 standard sieve, so that essentially all of the macroscopic bottom organisms could be recovered and transferred to vials of alcohol. The entire bottom of the pond was not representatively sampled. Even with hip boots it was impossible to get near the center of the pond because of the thick soft bottom deposits. The north edge of the pond was rocky and no bottom samples could be taken near shore. On the other hand, the five bottom samples taken on each visit were from a variety of depths and at scattered points so that the comoposite is believed to be a fair and representative qualitative and quantitative picture of the bottom fauna population.

Water samples for zooplankton counts were taken with a one-liter flask tied to a long pole, so that the flask was filled at a distance up to eight feet from the water's edge. Ten one-liter samples of water taken at random were considered to be a representative gross sample. The water was filtered through number 25 bolting silk, which is sufficiently fine to retain almost all zooplankters. The organisms were placed in vials of alcohol.

Qualitative collecting was also done along the shoreline and among the vegetation in order to get a more complete picture of the taxonomic groups involved in the economy of the pond.

Temperatures were taken regularly with a laboratory thermometer at a depth of 10 cm in water ranging from 30 to 80 cm deep. It was customary to take readings in several such places and derive an average.

CHEMICAL CONDITIONS

Several routine chemical determinations were made on the pond water, and in keeping with certain European studies, were found to be quite variable. Dissolved salts ranged from 21.5 to 48.1 mg per liter, and total organic matter 17.5 to 38.4 mg per liter. Bound carbon dioxide determinations were unusually high; they varied from 14.8 to 34.0 mg per liter. Most northern Colorado lakes and ponds of the alpine zone contain less than 10.0 mg per liter of bound carbon dioxide, and perhaps this is one factor that partially explains the unusually rich animal community occurring in the pond (at least *rich* as compared with other types of alpine ponds). Hydrogen ion determinations ranged from pH 6.5 to 7.3.

TEMPERATURE CONDITIONS

A preliminary visit to the pond was made on June 19, but the basin was completely obscured by snow and ice and there was no open water.

By June 29 the water temperature was 4.3°C, and the ice had disappeared from about half of the surface. Much of the bottom of the pond, however, was still covered with thick masses of ice. Trail Ridge Pond freezes solidly during the long winter, and the ice mass extends below the water-mud interface and well into the bottom deposits. The sudden spring melt of the pond ice first occurs at the surface and mid-depths, and the bottom layers apparently are insulated sufficiently so that melting is slower. It is possible for a layer of ice to remain on and in the bottom because it has intermingled aquatic plant roots and sufficient sand and gravel particles mixed in with it to give it weight and anchor it until the superimposed warm water thaws it out. Such bottom ice a common phenomenon in swift streams but is seldom reported from standing water.

By July 7 the water temperature at some distance from the edge of the pond had risen to 8.8°C, but snow and ice still remained along the north shore. By July 14 only a small amount of slush ice persisted on the north shore, and the average water temperature was 12.8°C.

Temperatures rose to a maximum of 16.1°C on July 29 and thereafter decreased slowly and irregularly. The first heavy snow fell on September 12, but the first ice appeared on the visit of October 12 when there was one-half inch along the east shoreline. The open water temperature was 5.5°C on this date. Slightly more ice was present on October 19 when the water temperature averaged 4.4°C. By October 29 the pond was frozen over except for a small area in the center; the ice was sufficiently thick to support a person's weight. The water temperature was 3.9°C. A few days later the Park roads were snowed in and closed to traffic until the following spring.

Thus in 1950 Trail Ridge Pond had an open season of about 120 days when the pond was either completely free of ice or only partially frozen over. In most years the season is considerably shorter. In 1951, for example, the pond was still completely covered with ice and snow on July 15, and in most

years it freezes over before October 15. Ninety or 100 days of open water is therefore probably more typical.

Because of the alternating cold nights and high insolation during daylight hours, wide daily temperature variations are to be expected in Trail Ridge Pond. Pesta (1933) found daily variations of 7 to 20°C in alpine ponds, and Pichler (1939a, 1939b) found daily variations of 6.5 to 30°C. At the periphery of Trail Ridge Pond where the water was less than 10 cm deep, temporary mid-day temperatures in sunny weather sometimes were 5, 10, or even 20°C above those taken in deeper water.

VEGETATION

Most tundra ponds have no true aquatic vegetation, perhaps because they usually dry up completely during much of the summer. Trail Ridge Pond, however, being permanent, supports a good emergent growth of the sedge, *Carex aquatilis,* along the east, south, and west shores. In a few places the sedge zone attains a width of 5 to 10 meters (fig. 3). The north shore has a rocky bottom unsuited to the establishment of rooted aquatics.

Carex undoubtedly provides additional ecological niches for the pond, for it was among these growths that the largest variety of metazoans, especially insects, was found.

BOTTOM FAUNA

The quantitative bottom samples contained only three groups of numerically dominant organisms: seed clams (*Pisidium*), tendipedid larvae (mostly *Tendipes, Calopsectra,* and *Procladius*), and small tubificid oligochaetes.

As shown in fig. 4, the tendipedid larvae were most abundant in the superficial bottom deposits early in the year, even before the surface ice had disap-

Fig. 3.—Trail Ridge Pond, looking west along the south shore.

peared. On June 29 an average population of 28 larvae per square meter was found. The water temperature was then only 4.3°C, and there was still a considerable amount of surface and bottom ice. The population increased enormously to 1512 per square meter by July 7 (water temperature 8.8°C), and 1904 on July 14 (water temperature 12.8°C). Thereafter the population dropped rapidly as the tendipedids pupated and quickly emerged as adults. On July 21 there were 1230 per square meter and on July 29 only 560. After August 16 the population varied irregularly and never exceeded 196 per square meter. Undoubtedly much of the irregularity of the curve in fig. 4 is produced by sampling errors. Thus Trail Ridge Pond had a simple unimodal annual curve for its tendipedid population. This is the usual situation in most temperate and subarctic lakes and ponds. It is quite possible, however, that one or more of the species represented had a two-year life cycle. Undoubtedly the larvae live at temperatures close to 0°C below the lower limit of ice in the frozen bottom during the long winter. With the rapid thawing of the water and bottom deposits in June and early July they migrate upward to the surface of the mud, where the great majority pupate and emerge as adults within two or three weeks. Although a few large larvae were found in the autumn just before the freeze, the great majority were undoubtedly in the egg stage or first larval instar, both of which will pass through the meshes of a number 20 sieve and escape detection. The second and third larval instars of many individuals were presumably attained during the winter and very early spring, even though temperatures were only 0 to 4°C. Thus it is difficult to avoid the conclusion that their threshold temperature for feeding and growth is exceptionally low. The occurrence of an abundance of active tendipedids on the bottom of most large cold lakes supports this familiar contention.

The *Pisidium* population curve (fig. 4) was strikingly similar to that for the tendipedid larvae, with a spring population burst which dropped off rapidly and remained at a low level from August through October. No *Pisidium* were collected on June 29 when there was still much ice on the pond, but by July 7 sufficient numbers had migrated to the surface layers from deeper parts of the mud to give an average population of 1162 per square meter. The maximum population, 1470 per square meter, was found on July 14. During the month following this peak the seed clams had a high mortality rate, and between August 16 and October 29 the residual population varied from 126 to 420 per square meter. Nothing is known about the reproductive habits of *Pisidium* in Trail Ridge Pond. A wide range of size was always found, but no one particular time was ever noted when there was a predominance of immature forms. It should be emphasized, however, that very young seed clams will pass through the meshes of a number 20 sieve and may thus have gone unnoticed. On the basis of our present knowledge of *Pisidium* biology, it is difficult to explain the occurrence of maximum numbers of large and mature individuals immediately after the ice melts in early summer. It is usually assumed that *Pisidium* is not active and does not ingest food while it hibernates below the mud surface during the cold months, but perhaps this assumption should be supported by actual observations. On the other hand, there certainly was not sufficient time between October 29 and the complete freeze of the pond a short time later to allow any appreciable growth in the late autumn.

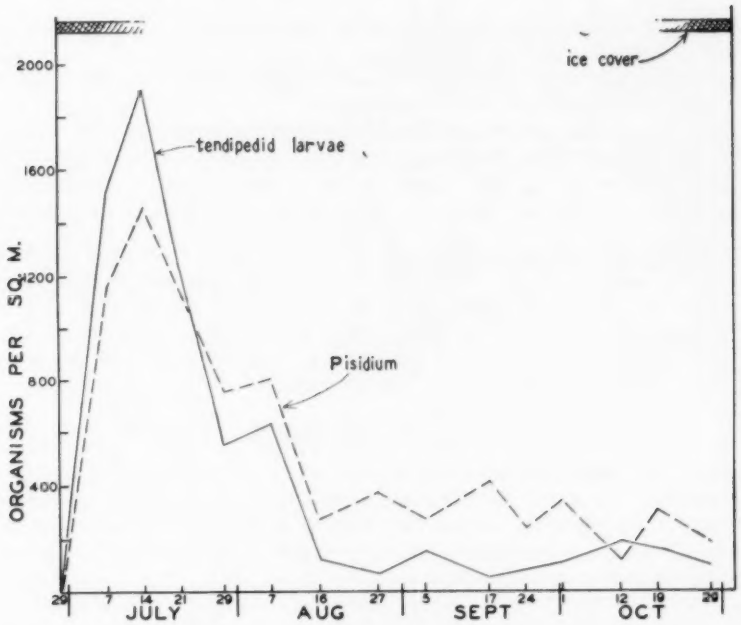

Fig. 4.—Seasonal population curves for tendipedid larvae and *Pisidium* in the bottom deposits of Trail Ridge Pond in 1950.

In keeping with the results obtained by many other investigators, it was found that the numbers of tubificid oligochaetes varied irregularly from place to place on the bottom and showed no distinct seasonal population trends. On several visits to the pond none were found in the five samples collected, and on October 1 a maximum of 168 individuals per square meter was collected. Oligochaetes apparently became active early in the season since 42 per square meter were found on July 7. Tubificids are notoriously difficult to sample quantitatively since many of them crawl through the meshes of the sieve and since they fragment very easily. Consequently the above figures are of little significance.

ZOOPLANKTON

The zooplankton population was exceedingly low, much lower in fact than those populations reported from the most barren of lakes. Copepod nauplii were the most abundant forms. On July 29 there was a peak of 121 individuals per liter, and on September 17 there were 9 per liter. On all other sampling dates there were negligible numbers of nauplii, or they were absent from the samples.

Small numbers of copepodid stages and adult copepods were found only occasionally, and it is obvious that there was a very high mortality of nauplii. The highest population of copepodids and adults occurred on September 17 when 0.9 individual per liter was taken. *Paracyclops fimbriatus* (Fischer) was

the only plankton species found, but a few specimens of *Canthocamptus* sp., a bottom dweller, were also collected.

Daphnia pulex was the only cladoceran taken; a total of only 11 individuals was collected on the 15 sampling dates.

Several *Pedalia fennica* and *Brachionus* sp. were the only rotifers taken in the plankton samples. Population densities were always less than one individual per liter.

PHYTOPLANKTON

Casual observations were made on the phytoplankton. Like the zooplankton, the population was qualitatively and quantitatively scanty, much more scanty than the phytoplankton of a typical large oligotrophic lake. Several species of diatoms, filamentous blue-greens, and *Cosmarium* were noted. Late in the season a *Spirogyra* bloom covered part of the bottom of the pond. Otherwise no special algal pulses were observed.

LITTORAL AND MISCELLANEOUS ORGANISMS

The following discussion includes organisms collected in random sweeps of a metal sieve among the submerged parts of sedges and along the shoreline. Few of these organisms ever appeared in the quantitative bottom samples or plankton samples. Since they were not homogeneously distributed, no quantitative estimates could be derived.

Beginning on July 21, peculiar greenish balls (superficially similar to *Nostoc* balls) were observed on the bottom and attached to the sedges below the water surface. These were found to be colonies of an unknown ciliate protozoan containing symbiotic (?) algal cells. Along with them in the colony were numerous diatoms and desmids, the entire colony being held together by a threadlike and gelatinous matrix. By July 29 the colonies nearly covered the submerged sedge growth as well as other objects along the shore. Thereafter they decreased in abundance but did not disappear until the end of the season. Presumably these colonies served as browse for many macrometazoans.

The fairy shrimp *Branchinecta shantzi* Mackin (formerly *B. coloradensis* Packard) was certainly the most abundant and most obvious macrometazoan in the pond. With the exception of a Texas report, this species is restricted to western high altitude lakes and ponds. It was abundant throughout most of the season, and although no definite quantitative estimates of the *B. shantzi* population could be made, the general population trends could be easily followed by inspection on the 15 visits to the pond. Overwintering undoubtedly occurs in the highly resistant winter egg stage, as is usual among phyllopods. On July 7 (the second visit to the pond) many phyllopod nauplii were present in the plankton. Two weeks later the first sexually mature adults appeared swimming about among the sedges near shore, and on July 29 the adult population reached a dense maximum. Thereafter the population declined and reached a minimum on September 5. This was followed by a second population increase which reached its maximum on September 24. On October 29, the last collecting date, a few stragglers still remained. Thus, Trail Ridge Pond appeared to have had two distinct generations of phyllopods in 1950. The two population peaks, one in late July and the other in late September, were of about equal density.

Phyllopods are most characteristic of vernal ponds which are dry during much of the year and in which a single population maximum per year is attained. Little appears to be known about their seasonal population variations in permanent bodies of water.

Branchinecta shantzi was clearly the most characteristic macrometazoan in Trail Ridge Pond. In their studies on mountain waters of Swedish Lapland, Brink and Wingstrand (1949) were impressed with a comparable situation, and they distinguished "*Lepidurus* pools," which are shallow mountain ponds characterized by an abundant notostracan phyllopod population. In their physical, chemical, and biological characteristics, *Lepidurus* pools are strikingly similar to Trail Ridge Pond.

Limnephilus larvae (Trichoptera) were associated with the submerged portions of the sedge plants, especially on July 29 and August 7. Thereafter the population fell off gradually until only scattered living individuals could be collected at the end of October. Their cases were constructed of variable amounts of sand, fine gravel, bits of vegetation, and *Pisidium* shells. It was a considerable surprise to find that living *Pisidium* also were used in the construction of *Limnephilus* cases. No other reported instance of the use of living seed clams has come to the attention of the present writers. In addition to *Limnephilus*, a single specimen of *Phryganea* was found.

Dytiscid beetles were nearly always found along the shore but were never abundant. Adult *Agabus* were collected on nearly all visits to the pond, but *Ilybius* were collected only in July and August. Larvae were found early and late in the season, but there was a rather long mid-season when none could be found. It can therefore be concluded that these beetles have a single generation per year with the larvae (and possibly eggs) overwintering in the bottom deposits.

Aquatic Hemiptera were taken occasionally in the shallows, especially *Arctocorisa sutilis*, *Sigara alternata*, and one species of *Notonecta*. A few water striders were observed as early as July 7 but were not collected.

Hydracarina were most abundant during August and September. Representatives of *Eylais*, *Lebertia*, and *Limnesia* were found.

Small numbers of certain Diptera larvae were taken along the shoreline that did not occur in the quantitative bottom samples. These included *Prionocera* (Tipulidae), *Stratiomyia* (Stratiomyidae), *Aedes* (Culicidae), and a case-building *Metriocnemus* (Tendipedidae).

The only vertebrates found at the pond were two mature mountain toads (*Bufo boreas boreas*). They were swimming about slowly in the slush ice on July 29 and July 14. On the latter date a large mass of toad eggs was found. Small tadpoles 15 to 20 mm long were later collected on August 16 but not seen subsequently.

DISCUSSION

The counterpart of Trail Ridge Pond does not appear to have been characterized in American hydrobiological literature. Blake (1945), however, briefly described "moraine ponds" in the Medicine Bow Mountains of Wyoming at an altitude of 10,200 feet. Such ponds have a longer ice-free season than Trail Ridge Pond and are surrounded by forests. They are also warmer and have a richer macrometazoan fauna, including several species of dragonfly and

damselfly nymphs, whirligig beetles, a variety of other beetles, leeches, and the swamp cricket frog.

McClure (1943) described several tundra ponds and small lakes at Churchill on Hudson Bay. In certain respects some of these resemble Trail Ridge Pond. They contained essentially all of the major taxonomic groups occurring in the latter except for seed clams. In addition, most of them contained snails, leeches, turbellarians, hydras, odonate nymphs, and ostracods. Numerically, however, the Churchill ponds were enormously richer in both numbers of individuals and in numbers of species. One pond, for example, contained up to 80,000 metazoans per cubic foot of water at the height of the season. Judging from McClure's meager temperature data, the Churchill tundra ponds attain higher summer maximum temperatures and have an open season about 30 to 50 days longer than that for Trail Ridge Pond.

Numerous European workers have described "Almtümpeln" which in many ways are similar to the Trail Ridge Pond type. They seldom contain phyllopods, however, but have a richer phytoplankton, cladoceran, and rotifer population.

Several important major taxonomic groups were not collected from Trail Ridge Pond. These include ostracods, amphipods, mayfly nymphs, odonate nymphs, and snails. All of these are common in ponds at elevations below 10,000 feet, and it is not clear whether low summer temperatures, the complete winter freeze, or some other ecological factors are of prime importance as limiting factors.

Some species are able to maintain themselves from year to year in the pond because of their ability to burrow deeply into the bottom deposits below the ice line. Examples are tendipedids, *Pisidium,* tubificid oligochaetes, and perhaps beetle larvae. In accordance with the investigations of Lindeman (1942) and others, however, it is quite probable that a large percentage of these organisms die during the long period of winter anaerobiosis. Most other groups overwinter in the resistant egg stage which withstands freezing in the superficial layers of the bottom deposits.

In general, most of the taxonomic groups in the pond were represented by exceptionally small numbers of individuals, and populations were much more scanty than those found in ponds and small lakes at lower elevations. The zooplankton, for example, was almost negligible, and with the exception of Trichoptera and *Branchinecta,* the miscellaneous organisms collected along the shallow margins were never abundant. Seldom could more than ten specimens of any one species be taken from five meters of marginal area.

Nevertheless, the dominant elements of the Trail Ridge Pond community are obvious. They are tendipedids, *Pisidium,* and *Branchinecta.* Judging from repeated observations on many plains and mountain ponds in Colorado, a *Branchinecta* population possibly does not make its appearance every summer in Trail Ridge Pond. More typically it may be absent for a year or two and then reappear for one, two, three, or more consecutive years. This irregular and intermittent annual occurrence of vernal and permanent pond phyllopods has been considered at length in Ohio by Dexter (1943) and Dexter and Kuehnle (1948, 1951).

Permanent ponds such as Trail Ridge Pond are common above timberline in northern Colorado. They occur invariably where they receive melting snow

water and rain seepage water from adjacent slopes. They range from 0.25 to 2.0 m in maximum depth, and their maximum dimensions range from about 5 to 100 m. Judging from casual observations made on many of them, the tendipedid—*Pisidium*—*Branchinecta* association is usually present.

A wide variety of temporary ponds and pools is also characteristic of the tundra, but these bodies of water are almost barren of macrometazoans and are not comparable with the permanent Trail Ridge Pond type.

SUMMARY

Trail Ridge Pond is a permanent body of water about 30 x 70 m and 1 m deep at an elevation of 11,500 feet in northern Colorado.

The plankton and bottom fauna were sampled quantitatively during the entire open season at intervals of 7 to 12 days from June 29 to October 29, 1950. Qualitative studies were also made on the macrometazoans living in the shoreline areas and *Carex* growths.

The pond freezes solidly during the winter, and the 1950 maximum summer temperature was 16.1°C on July 29. Dissolved salts ranged from 21.5 to 48.1 mg per liter. Hydrogen ion concentration determinations ranged from pH 6.5 to 7.3.

Zooplankton and phytoplankton populations were much more scanty than those in large barren oligotrophic lakes. Entomostraca and rotifers each averaged less than one individual per liter of pond water.

Tendipedid larvae and *Pisidium* (seed clams) attained their maximum abundance in the superficial layers of bottom mud just as the last of the ice was disappearing from the pond on July 14. The former reached 1904 individuals per square meter and the latter 1470. On June 29 only small numbers of tendipedids and no *Pisidium* were found, and it is concluded that there was a mass migration out of the deeper strata of the bottom deposits during the ensuing two weeks. Following July 14 the population tapered off to a level of 100 to 400 per square meter during September and October.

Tubificid oligochaete populations varied irregularly from 0 to 168 individuals per square meter.

The phyllopod *Branchinecta shantzi* was the most characteristic macrometazoan in the pond. It had a bimodal population curve, with distinct peaks on July 29 and September 24.

Small numbers of the following were present near the shoreline: *Limnephilus* larvae (Trichoptera); *Agabus* and *Ilybius* (Coleoptera: Dytiscidae); *Arctocorisa, Sigara,* and *Notonecta* (Hemiptera); Hydracarina; *Prionocera, Stratiomyia, Aedes,* and *Metriocnemus* larvae (Diptera).

The dominant and characteristic organisms of Trail Ridge Pond are the tendipedid-*Pisidium-Branchinecta* community.

In general, the pond has an impoverished fauna, both qualitatively and quantitatively, and it is believed that the very short open season and the complete winter freeze of the water mass are important contributing factors.

Trail Ridge Pond is compared with other subarctic and mountain tundra ponds in both North America and Europe.

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The Location of the Contact Chemoreceptors of the Cherry Fruit Fly, Rhagoletis Cingulata and the Flesh Fly, Sarcophaga Bullata[1]

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In the Diptera, tarsal contact chemoreceptors have been found in the following species: *Phormia regina, P. terraenovae, Phaenicia sericata, Calliphora vomitoria, C. vicina, Cynomyopsis cadaverina, Callitroga macellaria, Stomoxys calcitrans, Musca domestica, Drosophila melanogaster, Tubifera sp., Tabanus sulcifrons* (references to original studies in Frings and Frings, 1949) and *Aedes aegypti* (Frings and Hamrum, 1950). These represent only six families of this large and important order of insects. Tarsal chemoreceptors have been reported as being absent in *Rhagoletis pomonella*[2] (Trypetidae) by Middlekauf (1941), the only species of fly tested so far in which these receptors have not been found.

Labellar contact chemoreceptors have long been assumed to exist in the Diptera. They have been proved to exist, however, only in *Phormia regina, Calliphora vomitoria, C. vicina, Phaenicia sericata, Musca domestica, Tubifera sp., Tabanus sulcifrons* (Frings and Frings, 1949) and *Aedes aegypti* (Frings and Hamrum, 1950). No exceptions have been reported for any flies tested.

The present paper reports studies on two species of Diptera—the cherry fruit fly, *Rhagoletis cingulata* (Trypetidae) and the flesh fly, *Sarcophaga bullata* (Sarcophagidae). Studies on the first species test the possibility that this may represent an exception to the rule in Diptera. Studies on the second add data on the location of contact chemoreceptors in a species from a family whose members have not previously been tested.

Materials and Methods.—The *Rhagoletis cingulata* adults used in these experiments were hatched in the laboratory from field collected pupae. These were collected and sent to us by Dr. James A. Cox, of The Pennsylvania Agricultural Experiment Station, and we wish to express our appreciation to him for this favor. Twenty-five adults were used (13 ♂♂ and 12 ♀♀). These were mounted on wax blocks on the ends of glass rods, as described previously (Frings, 1947). While mounted, they were given water followed by 1 M sucrose solution every 24 hours. Longevity was good under these conditions, a fact which may be surprising considering the small size of the subjects.

Tests were carried out each day after the animals had been given water, and before they were fed. The local stimulation method previously described in detail (Frings and Frings, 1949) was used. An artist's brush moistened with water was touched to suspected loci of end-organs (labella and tarsi) and the reaction noted. Since the animals had previously been given all the

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2 In our review (1949) this was incorrectly reported as being for *R. fausta* and *R. cingulata* also.

water they would take, this represented a reaction to a non-sapid stimulus. Following this an artist's brush moistened with 1 M sucrose solution was similarly brought to the suspected loci and the reaction noted. The specific response used as an index of reception for this species was the dropping of the proboscis of the fly which precedes feeding. Each fly was tested at least four times each day and the total records for each fly each day were combined into one testing record. Under these conditions, there were three possible reactions: 1) a clear-cut proboscis response; 2) no response to sugar solution but feeding later when the solution was brought to the mouth-parts; 3) no response at all even when sugar solution was brought to the mouth-parts. The first indicates reception by the suspected part, the second indicates no reception by the part, and the third indicates that the fly is unresponsive and therefore not suitable for study at that time.

A total of 98 testing records, each representing at least four tests, were thus obtained with intact flies. After that, the fore-tarsi were removed to facilitate testing the other tarsi. This operation was performed without anaesthesia by means of fine microscalpels.

The adults of *Sacrophaga bullata* used in the tests were laboratory reared from a captive caged stock. For tests on intact animals, over 200 mounted individuals were used. The methods used for determining the exact location of the receptors were the local stimulation methods as detailed above for *Rhagoletis,* except that 1.5 M sucrose solution was used as the test substance. Extension of the proboscis was used as the index of reception. For more precise localization of the receptors involved the fore-tarsi and middle tarsi of 35 mounted flies were removed with microscalpels segment by segment, and the flies tested after a recovery period.

RESULTS

The adult fruit flies responded regularly by dropping the proboscis when the labella were touched with a brush bearing 1 M sucrose solution. This reaction was clear-cut and occurred uniformly, unless the flies did not feed at all at the testing period, a rare occurrence. After the first day or two, the flies fed well, and the labellar reaction was striking. No attempt was made to determine the exact end-organs on the labella, but they are probably trichoid sensilla. The proboscis response could be elicited by touching only these hairs without touching the labellar surface.

The evidence for receptors on the tarsi of at least the fore-legs was equally clear-cut. Only 7% of the total testing records were negative when the tarsi were touched with a brush moistened with 1 M sucrose solution. With care, one could touch only the fore-tarsi, without having the other tarsi brought to the brush. Under these conditions equally clear-cut responses were obtained. It was not possible to touch the middle or hind tarsi without having the front tarsi brought to the brush almost immediately, so that these could not be tested on intact animals. The fore-tarsi were removed, therefore, but after this operation the flies moved the proboscis in and out almost incessantly. Under these circumstances critical experiments were impossible. We can conclude, therefore, only that the fore-tarsi have contact chemoreceptors. Their exact location on these was not determined.

The adult *Sarcophaga bullata* showed similar clear-cut reactions to a 1.5 M

sucrose solution applied to the labella. Hundreds of tests were made and the evidence is overwhelming that chemoreceptors are present on the labella. So far critical experiments have not been performed to determine the exact end-organs, but it is clear that sensory hairs (trichoid sensilla) are involved. Touching them alone with sucrose solution without touching the surface of the labella elicits the proboscis response.

That tarsal contact chemoreceptors are also present is a certainty. It is so simple to demonstrate these by merely touching the tarsi of water-sated flies to sucrose solutions that we use these flies to demonstrate the phenomenon to students in elementary courses in zoology. Beverly Cox, a graduate student in this department, has used this species for studies on the physiology of tarsal contact chemoreception and has checked these results also.

Local contact experiments showed clearly that the fore-tarsi at least were involved. It was impossible, however, to touch the other tarsi without having the fore-tarsi brought to the brush at the same time. Removal experiments were performed, therefore, to locate the receptors more exactly. Removal of the fore-tarsi left the reaction to tarsal contact unimpaired. Removal of the fore and middle tarsi abolished the reaction, if 1.5 M sucrose solution were used as the stimulating agent. Proboscis extensions, however, occurred in a few flies if moistened sugar cubes were used as the test stimulus. Contact chemoreceptors are clearly present on the fore and middle tarsi. If they are present at all on the hind tarsi, they have much lower sensitivity than those on the other two pairs of legs.

The end-organs involved in contact chemoreception on the tarsi were localized more exactly by excision of segments of the tarsi followed by touching with a brush dipped in sucrose solution or by dipping the legs in the solution. There are five segments on the tarsus of this species. Removal of the terminal four segments of the fore-tarsi one by one, in flies from which both middle and hind legs had been removed, did not abolish the response. Removal of the terminal four segments of the fore-tarsi with simultaneous removal of the distal 1/4 of the basal segment, however, did abolish the response. It is thus clear that the receptors are present at least on the distal part of the proximal segment of the fore-tarsus. They are probably present on the terminal four segments also. Local stimulation tests showed them to be present at least on the terminal two segments. Dipping the tarsi in sucrose solution only to the depth of the terminal two or three segments also showed receptors to be present somewhere on them. With the terminal two segments removed, it was possible to touch the second and third segments with a brush moistened with sugar solution or to dip them in sugar solution without contacting the proximal segment. In these cases, positive reactions occurred also. The evidence seems good, therefore, that the chemoreceptors exist on the terminal four segments and the distal 1/4 of the basal segment of the fore-tarsi.

With the middle tarsi the same kind of excisions and tests were performed as with the fore-tarsi. In this case, however, evidence of reception disappeared with removal of the terminal three segments and the distal 2/3 of the second segment. There was no evidence that the proximal segment of the tarsus bore contact chemoreceptors. These receptors, therefore, were found only on the terminal four segments of the middle tarsi.

With the hind tarsi the inconsistent responses, occurring only in a few

flies when the tarsi were in contact with moistened sugar, made it impossible to decide whether contact chemoreceptors were present at all. Thus no experiments on localization could be performed.

DISCUSSION

The results obtained with *Rhagoletis cingulata* are obviously at variance with those obtained by Middlekauf (1941) for *R. pomonella*. That this is a species difference seems unlikely, for these species are very similar. It is more likely that the "10% honey solution," used by Middlekauf, was not sufficiently concentrated to elicit proboscis responses. While it is impossible to know the concentration of his solution, the approximate concentration can be calculated from the average composition of honey (Butler, 1949). Such a calculation shows that a solution made by adding 9 parts of water to 1 part of honey would be approximately 0.2-0.3 M with respect to glucose and fructose. The sucrose content would be very low and probably negligible. The threshold for glucose for most insects is quite high. That for fructose may be as high as for glucose and generally is not so low as that for sucrose. It is quite possible, therefore, that the "10% honey solution" used by Middlekauf was not sufficiently concentrated to elicit proboscis responses from the tarsal chemoreceptors. It seems fair to conclude that, since *Rhagoletis cingulata* has tarsal contact chemoreceptors, *R. pomonella* almost certainly has. At least the genus, *Rhagoletis,* does not constitute a complete exception to the rule among Diptera.

The present study adds data on the contact chemoreceptors of two more species of Diptera representing two more families, thus bringing the total tested so far to eight families. This sample is still small when considered in relation to the whole order, but certainly tarsal and labellar contact chemoreceptors seem to be rather generally distributed in the group. It would be interesting to test flies, such as robber flies (Asilidae) or louse flies (Hippoboscidae), with habits quite different from those of the flies tested up to now. These might be expected, from their habits, to lack tarsal chemoreceptors. Most other Diptera, however, must probably be assumed to possess them, although only critical experiments on numerous species will enable us to decide just how widespread in the order these receptors are.

SUMMARY

The loci of contact chemoreceptors in *Rhagoletis cingulata* and *Sarcophaga bullata* were determined by local stimulation methods accompanied by removal of suspected locations. *Rhagoletis cingulata* has these receptors on the labella where they are probably trichoid sensilla, and on the tarsi of at least the forelegs. *Sarcophaga bullata* has the receptors on the labella where they are also probably trichoid sensilla, and on the terminal four segments and the distal 1/4 of the basal segment of the fore-tarsi and the terminal three segments and distal 2/3 of the second segment of the middle tarsi. Results with the hind tarsi of *Sarcophaga bullata* were inconclusive. In the Diptera, contact chemoreceptors have so far been shown to be present on the tarsi in 15 species from 8 families and on the labella in 10 species from 7 families.

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Notes on some Eastern North American Psocids with Descriptions of two new Species

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The two new species described below were discovered in the course of studying the Indiana psocid fauna. Both are widely distributed in eastern North America.

The male of *Caecilius aurantiacus* (Hagen) is described here for the first time, and the genitalia of *Echmepteryx hageni* (Pack.) are figured for the first time.

Lepidopsocidae

The taxonomy of this family is in need of revision, but it appears that the group separated off as Lepidillidae by Enderlein (1906), the type genus of which was placed again in the Lepidopsocidae by Pearman (1936) is a natural division of the Lepidopsocidae. Short forewings and lack of hindwings are characteristic of the group, but one individual of the new species is an exception. The genera *Pteroxanium* End., 1922 (= Lepidilla Rib., 1905 preoccupied), *Lepolepis* End., 1906, and perhaps *Cyptophania* Banks, 1931 and *Pteroxaniella* Karny, 1932, belong to this group. I place the new species described below in *Lepolepis* with reservations.

Lepolepis Enderlein, 1906.

Genotype.—*L. ceylonica* Enderlein, 1906. Spolia Zeylanica 4:112.

This genus has to date apparently been known only from the type series of the genotype, two females, from Perodeniya, Ceylon.

Lepolepis occidentalis sp. nov.

Diagnosis.—Resembles *L. ceylonica* in general body form, relative size of forewings in short-winged form, and presence of a stout, long subapical seta on second and third segments of maxillary palpus. Differs from *Pteroxanium kelloggi* (Rib.) in its much shorter fore winglets, lack of hindwing rudiments, and presence of the stout subapical palpal setae (lacking in *P. kelloggi* according to Enderlein). Resembles both *L. ceylonica* and *P. kelloggi* in form of the hind tarsal claw and in possession of a three-pronged tip of the maxillary rod. Eyes much larger than those of *L. ceylonica*. Body and winglets densely clothed in closely appressed light golden brown scales. Head more sparsely covered with upright scales producing a shaggy appearance. Vertex and frons marked with dark brown; apparently unmarked in *L. ceylonica*, and marked with a much more complex pattern in *P. kelloggi*.

Holotype female.—Long-winged with well developed hindwings and venation. Measurements: Total body length 2.16 mm; forewing length 1.85 mm (maximum width 0.45 mm); hindwing length 1.51 mm (maximum width 0.39 mm); antennal length 1.88 mm; hind tibial length 0.76 mm; hind tarsus (t_1 0.25 mm, t_2 0.06 mm, t_3 0.06 mm). Head: Eyes rounded externally with straight internal margins; placed at hind angles of head. Occipital and frontal sutures conspicuous. Clypeus bulging. Vertex, frons, and sides of clypeus sparsely clothed in rather long, slender, upright, curving scales; a conspicuous patch of scales on right half of frons immediately above clypeus. Remainder of clypeus bearing decurved hairs. Mouthparts similar to those of paratypes (see below). Thorax: Pronotum a rather narrow, transverse ridge divided in middle by a conspicuous suture and divided half-way between this and each side by a pair of weak sutures

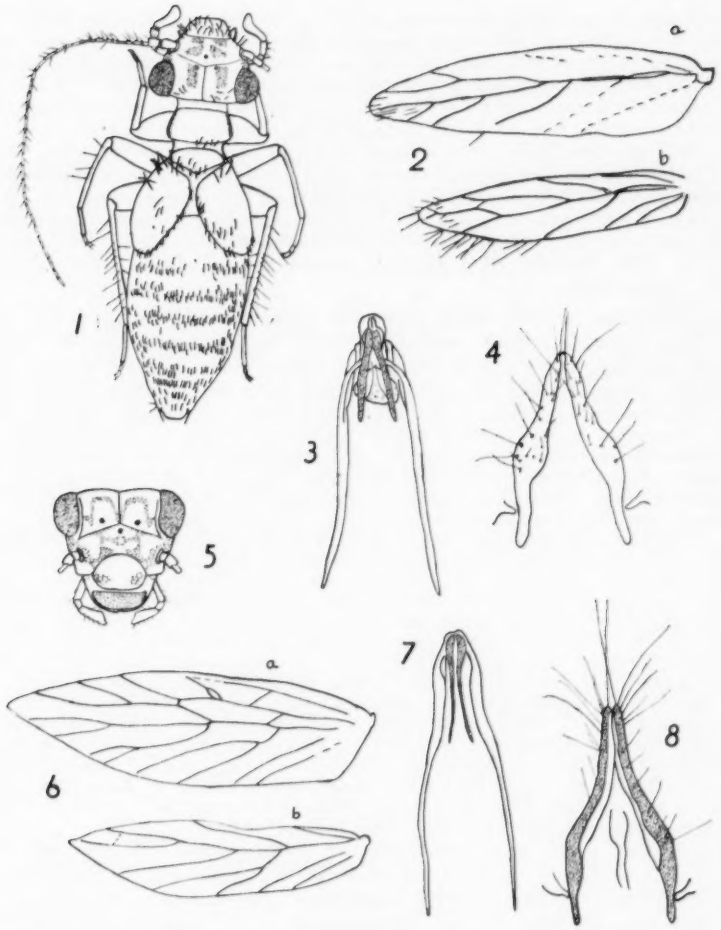

Plate 1.—Figs. 1-8—1-4. *Lepolepis occidentalis* sp. nov. 1. paratype ♀; 2. holotype ♀, a. forewing, b. hindwing; 3. paratype ♂, copulatory apparatus; 4. holotype ♀, gonapophyses. 5-8. *Echmepteryx hageni* (Pack). 5. ♀, head, anterior view; 6. ♀, a. forewing, b. hindwing; 7. ♂, copulatory apparatus; 8. ♀, gonapophyses.

each separating off a lateral lobe bearing numerous pits which are probably scale attachment points. A few curved, upright scales remaining along hind margin. Mesonotum almost scaleless, roughly diamond-shaped with forewings attached below lateral angles. Forewings (Pl. 1, fig. 2a) extending beyond tip of abdomen, with no closed cells; covered with slender appressed scales probably many of which have fallen off; scales long at apices. Membrane clear; anal cell slightly pigmented. Hindwings (Pl. 1, fig. 2b) with one closed cell in left wing, none in right. Coxae large, meeting along mid-line. Tibiae and tarsi long and slender. Hind tibiae bearing several slender upright setae. Abdomen: segments 2 to 7 membranous and covered with closely appressed golden brown scales. Segments 1, 9, 10, and tergite of 8 sclerotized. Paraprocts each with an apically attached 'anal appendix' in the form of a long, rather stout seta. Gonapophyses (Pl. 1, fig. 4) of

usual form for the family, rather stout, setiferous. COLORATION (in alcohol): Ground color tan marked with dark brown much as in Pl. 1, fig 1, but three light spots associated with the three black spots on vertex and frons. Clypeus bordered laterally with dark brown. Eyes black. Thorax light brown, slightly darker than ground color of head. Legs concolorous with thorax. Abdomen pale in membranous area; terminalia approximately concolorous with thorax. Paraprocts suffused with dark brown.

Allotype male.—Differs from holotype as follows: forewings not exceeding second abdominal segment, their venation reduced to two faint indications of veins; hindwings absent; mesonotum with a straight anterior margin; no light spots associated with black spots on head; thorax, terminalia, and legs paler, approximately concolorous with pale abdomen; pronotum bordered with dark brown; winglets bearing a few long, slender upright scales. Genitalia (Pl. 1, fig. 3, of paratype; those of allotype similar) of usual form for the family.

There can be little doubt about the association of this male with the holotype female. It agrees very closely with the holotype in the distinctive head markings and shape of the apical joint of the maxillary palpus, also females taken with the allotype agree closely with the holotype in genitalia.

Paratypes.—All paratypes are short-winged and similar to the allotype, differing from the holotype in the same ways as does the allotype. Mouthparts (studied in detail on paratypes): Mandibles of usual form for the family; lacinia tridentate at apex; terminal segment of maxillary palpus long and axe-shaped. Distribution of conspicuous setae on maxillary palpus: one at about middle of second segment, one or two at apex of second segment, one in a group of smaller setae near apex of third segment.

Collection data: Holotype female.—INDIANA: Dunes State Park (Porter Co.), August 15, 1950, sifting a branch of dry leaves on a sand dune above the beach, D. W. Rice and E. L. Mockford. *Allotype male.*—INDIANA: Bloomington (Monroe Co.), July 4, 1951, ground litter in sassafras grove, University Forest, E. L. Mockford. *Paratypes*—INDIANA: Bloomington, same data as for allotype, 15 ♂ 8 ♀; Bloomington, July 7, 1951, ground litter in young upland woods, University Forest, 13 ♂ 9 ♀, E. L. Mockford; Michigan City, August 15, 1950, dry oak leaves on sand dune, ♂ ♀, D. W. Rice and E. L. Mockford. Alabama: Monte Sano Overlook, August 19, 1951, in ground litter on hillside, 3 ♂, E. L. Mockford. *Other records,* INDIANA: Bloomington, 5 nymphs taken with allotype; 1 nymph taken with paratypes July 7, 1951; McCormick's Creek State Park (Owen Co.), July 8, 1951, ground litter in young upland woods, 2 nymphs, E. L. Mockford. MICHIGAN: Branch Co., ½ mile north of Indiana line on U. S. Highway 27, July 5, 1950, sifting ground litter in oak-hickory woods, 2 nymphs, D. W. Rice and E. L. Mockford. FLORIDA: Niceville (Okaloosa Co.), August 21, 1951, in dry ground litter under live oak, nymph, E. L. Mockford.

Distribution of type material.—The holotype and allotype will be deposited in the U. S. National Museum. Paratypes will be deposited in the collections of the following institutions and individuals: Museum of Comparative Zoology, K. M. Sommerman, J. V. Pearman, and E. L. Mockford.

ECHMEPTERYX HAGENI (Packard)

Since this species might possibly be confused with the long winged form of the above species (as was done in my 1950 paper), figures of the distinctive head markings (Pl. 1, fig. 5) and wing venation (Pl. 1, fig. 6) are here given. I also include figures of the genitalia of both sexes (Pl. 1, fig. 7 of ♂, fig. 8 of ♀) as they have never been published.

Caecilius sommermanae sp. nov.

CAECILIUS AURANTIACUS Chapman, 1930 (in part) *non* Hagen, 1861.

Diagnosis.—Similar to *C. aurantiacus* (Hagen), differing in its slightly smaller size paler coloration, pale ocellar intervals, lack of a definite pair of spots on the pro- and mesonotal lobes, distribution of dark pigment in the wing veins, structural details of genitalia and 'telson lobes,' ratio of optic interval to diameter of eye (IO/D).

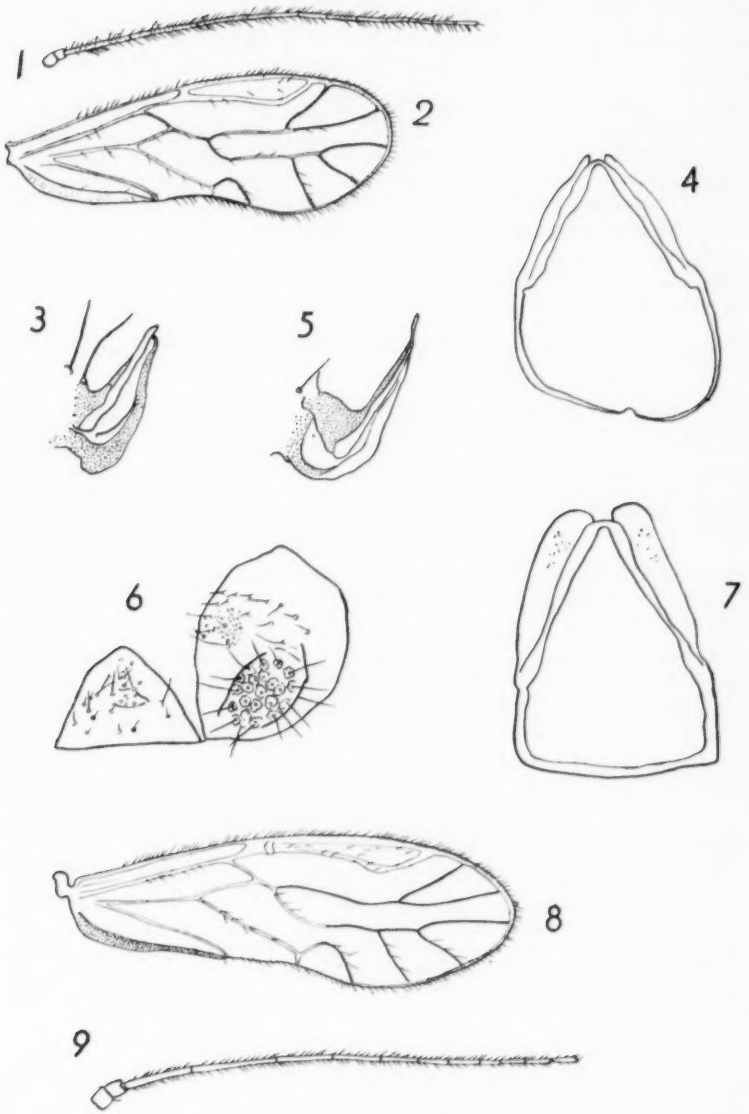

Plate 2.—Figs. 1-9 Caecilius.—1-4. *C. sommermanae* sp. nov. paratype 1. ♀, antenna; 2. ♀, forewing; 3. ♀, gonapophyses; 4. ♂, phallic frame. 5-9. *C. aurantiacus* (Hagen) 5. ♀, Gonapophyses; 6, ♂, epiproct and paraproct; 7. ♂, phallic frame; 8. ♀, forewing; 9. ♀, antenna.

Holotype male.—MEASUREMENTS: Total body length 1.93 mm; forewing length 2.46 mm (maximum width 0.98 mm); hindwing length 1.82 mm (maximum width 0.62 mm); antennal length 2.35 mm; hind tibial length 0.78 mm. MORPHOLOGY: Eyes large and bulging; vertex narrow between eyes (IO/D=0.44). Antennal ciliation rather long (as in Pl. 2, fig. 1 of paratype female). Venation (Pl. 2, fig. 2 of paratype female): fusion of R and M long. M strongly downcurved from the fusion. Cell R_{4+5} uncurved. Anal vein lacking ciliation. Parameres (Pl. 2, fig. 4 of paratype) acute at apices. COLORATION: body generally pale yellow; thorax somewhat darker. Eyes black. Ocellar intervals pale, concolorous with surroundings. Veins in apical half of forewing dark except for R_1, base of cubital loop, and radial petiole (which is dark at its base and apex). Wing membrane almost colorless. Pterostigma white.

Allotype female.—Similar to holotype but larger and eyes much smaller in proportion. MEASUREMENTS: Total body length 2.13 mm; forewing length 2.69 mm; antennal length 2.46 mm; IO/D=1.33.

Gonapophyses (Pl. 2, fig. 3 of Paratype) rather short; rudimentary lateral bearing two hairs.

Paratypes.—Female paratypes from Indiana have IO/D somewhat lower than in the allotype (in four specimens measured, IO/D=1.28 in three, 1.14 in one), but are otherwise similar to the allotype. Many paratypes have the anal cell in the forewing brown. The male telson lobes were studied in detail on two paratypes and no fields of papillae were found. Some geographical variation occurs. Some of the specimens from Washington, D. C. and all of the material from Alachua County, Florida have dusky wings but are otherwise similar to the pale-winged form.

Collection data: Holotype.—DISTRICT OF COLUMBIA: Washington, Rock Creek Park, June 15, 1947, beating shrubs, K. Sommerman. *Allotype female.*—Same data as for holotype.

Paratypes.—CONNECTICUT: Mount Carmel, October 12 and 14, 1941, beating Red Pines, 13♂, 31♀, K. M. & A. H. Sommerman. DISTRICT OF COLUMBIA: Washington, Rock Creek Park, June 15, July 20, August 19 and 23, September 10 and 16, 1947; October 6, 8, and 20, 1951, beating and sweeping shrubs, sifting ground litter, beating dried leaves, on Beech Tree trunks, and on rocks, 11♂ 40♀, K. M. Sommerman. FLORIDA: Alachua Co., Devil's Millhopper, May 10, 1952, sweeping vegetation, 5♂ 3♀, E. L. Mockford; Newman's Lake, February 29, 1952, beating Cabbage Palm fronds, 2♂ 2♀, E. L. Mockford; San Felasco Hammock, March 7, 1952, on Magnolia leaf, ♀, E. L. Mockford; Liberty Co., Torreya State Park, June 3 and 4, 1952, beating Needle Palm fronds, Torreya trees, dry oak leaves, and Cane, 3♂ 16♀, E. L. Mockford. INDIANA: Bloomington, October 22 and 29, 1949, sweeping spruces and pines in University Forest, ♂ 9♀, E. L. Mockford; Shades State Park, September 11, 1950, beating dried leaves, branches of deciduous trees, and Hemlocks, 3♂ 9♀, E. L. Mockford; Turkey Run State Park, September 11 and 12, 1950, beating Hemlocks and deciduous trees, 6♀, E. L. Mockford; Winona Lake, June 30, 1947, sweeping foliage, ♂ 2♀, E. L. Mockford. TENNESSEE: Great Smoky Mountains National Park, July 10, 1949, sweeping Hemlocks, ♂ 2♀, E. L. Mockford. WEST VIRGINIA: Lost River State Park, October 9 and 13, 1950, ♂ ♀, B. D. Burks.

Distribution of type material.—The holotype and allotype will be deposited in the U. S. National Museum. Paratypes will be deposited in the collections of the following institutions and individuals: U. S. National Museum, Museum of Comparative Zoology at Cambridge, Mass., K. M. Sommerman, and E. L. Mockford.

This species is named in honor of Dr. Kathryn M. Sommerman, who has done much work on North American psocids. Dr. Sommerman very kindly loaned me her material of this species.

Discussion.—Chapman's description of *Caecilius aurantiacus* (1930, Pg. 320) includes two species. The male is *C. sommermanae sp. nov.* as is clearly shown by his figure of the male genitalia. It therefore became necessary for me to establish the identity of *C. aurantiacus*. At my request, Dr. P. J. Darlington of the Museum of Comparative Zoology, Harvard College, examined the type of *C. aurantiacus* with reference to diagrams of head and wing characteristics of females of the two species. He informs me that it has dark ocellar intervals, small and well separated eyes (hence Hagen's determination of its sex as female is surely correct), and apparently no interrupted pattern in the dark apical veins of the forewing. In the original description of *Psocus aurantiacus*, Hagen mentions four cloudy brown spots in the thoracic tergites. The species represented by Chapman's female possesses all of these characters and is therefore with little doubt *C. aurantiacus* (Hagen).

CAECILIUS AURANTIACUS (Hagen)

As shown above, the male of this species has not been described. It is similar to the female in size and color pattern but is frequently darker and has much larger eyes. The phallic frame (Pl. 2, fig. 7) differs markedly from that of the preceding species, especially in its possession of blunt-tipped parameres. The epiproct and paraprocts (Pl. 2, fig. 6) bear fields of papillae.

The female gonapophyses (Pl. 2, fig. 5) are long and pointed at the tips; the rudimentary lateral bears a single hair. For the female used in the figure of gonapophyses, I0/D=2.

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A Parasitological Study on Navy Recruits*

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Chandler (1949) points out that the science of parasitology "really came of age" during World War II. The many evidences of this growth are reflected only partially in the number of surveys of parasitic incidence among military personnel in many parts of the world. Many surveys were made during and shortly after World War II—some in military hospitals, others among prisoners of war, and others among personnel being released to inactive duty.

Since the problems attendant upon parasitic infection were brought to the fore usually *after* the service man had left his training area, it was thought desirable to determine the relative amount of infection *prior* to completion of basic training. Sapero and Johnson (1939) found a significant difference in the percentage of infections among Navy recruits from the southern states compared with those from other states. These authors concluded that most infections with *Endamoeba histolytica* were acquired prior to naval service. Michael (1946) further concluded that amebic infections among returning service men do not constitute a public health problem. Taylor (1951), in a survey of 991 Marine Corps personnel found a low combined incidence (1.3 per cent) of *Endamoeba histolytica*. The same investigator found no significant difference in hookworm infection between overseas and non-overseas personnel, but a highly significant difference between individuals from the southern coastal states against all other states represented. In the present study it was thought desirable to determine if the incidence of parasites in select group of servicemen who had not yet completed recruit training varied from that among other groups studied.

ACKNOWLEDGEMENTS

The survey extended from June to September 1952, while the author was on temporary active duty in the U.S. Naval Reserve.

The author wishes to thank CDR John R. Seal, MC, USN, Medical-Officer-in-Charge of NMRU-4, and his staff for the aid and excellent facilities afforded for the investigation. Appreciation is particularly expressed to W. L. Harper, HM2, USN, who assisted in the collection of samples at Great Lakes. Samples from the Bainbridge Naval Training Center, Bainbridge, Maryland, were collected and sent to the author at Creighton University where the observations were completed. Thanks are also expressed to Captain R. M. McComas, MC, USN, Medical Officer, U.S. Naval Training Center, Bainbridge, Maryland, for cooperating in obtaining the Bainbridge material and to Manfred Froehlich, HM3, USNR, who collected and forwarded the samples. Dr. Leo Kennedy, Chairman, Department of Education, Creighton University, kindly made suggestions regarding interpretation of the data. Rita Ann Kisicki assisted in the technical work and the preparation of the report at Creighton University.

Appreciation is finally expressed to the Regimental, Battalion, and Company Commanders at both Naval Training Centers who cooperated fully in procurement of samples for study.

* The opinions expressed herein are those of the author and cannot be construed as reflecting the views of the Navy Department or of the Naval Service at large.

MATERIALS AND METHODS

The survey was initiated in June, 1952. Recruits were selected within three weeks of entrance to recruit training. A questionnaire was prepared for each man examined, identifying the examinee. Information concerning age, type of employment, name and population of his home town, etc. (below or over 2500) was also obtained. In an attempt to ascertain if there was a significant difference in parasitic incidence among recruits from the middle western areas and those from the southeastern United States, the total sample was divided into two groups. The middle west (MW) group included recruits from the Dakotas, Minnesota, Wisconsin, Illinois, Indiana, Ohio, and Iowa. The southeast (SE) group included recruits from the District of Columbia, Maryland, West Virginia, the Carolinas, Georgia, Alabama, Florida, Tennessee, Kentucky, Mississippi, and Louisiana. A total of 513 recruits from the midwestern states and 496 from the southeastern states were examined for intestinal parasites.

Fecal samples were collected in sputum cups and preserved in 10 per cent formalin. It was possible to collect 539 samples at Great Lakes from June to September, 1952. The remaining 470 specimens were collected in September at Bainbridge, and sent to the author at Creighton University where the study was completed. The zinc-sulfate-centrifugal-floatation technic was employed to concentrate cysts and helminth ova on 90 per cent of the specimens. The AEX and alcohol sedimentation technics were utilized for the remaining 10 per cent, as a comparative study of technics. In addition to these methods, a direct smear was examined for each specimen. All preparations were stained either with Lugol's iodine solution, or with the MIF stain suggested by Sapero, Lawless, and Strome (1951).

TABLE 1.—Incidence of parasites in two groups of Navy recruits

	MW (513)		SE (496)			
Protozoa	Number	Per Cent	Number	Per Cent	Total	Average Per Cent
Endamoeba coli	38	7.4	44	8.9	82	8.13
Endolimax nana	41	8.0	52	10.5	93	9.22
Endamoeba histolytica	20	3.9	26	2.5	46	4.55
Giardia lamblia	14	2.7	12	2.4	26	2.57
Iodamoeba butschlii	11	2.1	8	1.6	19	1.88
Chilomastix mesnili	4	0.78	6	1.2	10	0.99
TOTALS	128	24.88	148	29.8	276	27.35
Helminths						
Necator americanus			8	1.6		
Ascaris lumbricoides			3	0.6		
Trichuris trichiura			2	0.4		
Strongyloides stercoralis			3	0.6		
Hymenolepis nana			1	0.2		
			17	3.4		
TOTALS	128	24.88	165	33.2	293	29

In addition a survey of oral protozoa was made on 539 recruits at the Great Lakes Naval Training Center. Culture methods for diagnosis were utilized. A single oral sample from each recruit was obtained with a cotton swab, with especial effort to remove material coating the gingiva and teeth. Specimens were taken at reveille before the recruits had opportunity to bathe or brush their teeth. Specimens thus procured were incubated for 24 hours at 38°C in test tubes on nutrient agar slants overlaid with a Ringer's-egg-white solution. Observation was then made for oral protozoa.

An average of 2.5 pinworm examinations per man was made on 539 recruits. The scotch cellulose tape method of obtaining specimens was found to be fast, efficient, and reliable. A loop of 1 inch tape 2½ inches long was applied to the perianal region and this tape placed on a glass slide in each examination. Specimens were taken at reveille and observed on the same day.

RESULTS AND DISCUSSION

The incidence of protozoan and helminth intestinal parasites is presented in table 1. Of 1009 recruits examined, a total of 276, or 27.35 per cent was found to harbor protozoan parasites. A total of 293, or 29 per cent, was found to be infected with protozoan and/or helminth parasites. It is significant that the only helminth infections were found in the group from the southeastern area of the United States.

Three of the six protozoan infections found (*E. nana, E. coli,* and *E. histolytica*) were found in greater numbers in the southeastern group. On the other hand, the other three (*G. lamblia, I. butschlii,* and *C. mesnili*) were slightly more abundant in the midwest group. Application of the student's "t" test to the differences in numbers found in each group was in no case significant. For example, the "t" ratio was 1.03 in the case of comparative incidence of *E. histolytica.* This ratio represents only the 32nd degree level of confidence and obviously is not significant. It is felt that a trend is represented, however, and that the examination of a larger sampling might show a trend toward a significant difference.

The over-all incidence of most species is less than that usually listed from surveys of the general population and less than that given by Sapero and Johnson (1939). Reasons for this lower incidence are perhaps threefold. First, a select age group is involved. Ninety per cent of the recruits examined were in the age group 17-20; only 10 per cent were 21 or older. Second, as Taylor (1951) points out, the generally high standards of sanitation and health in the service, plus accelerated public health programs among civilians may be important factors in a lowered incidence of parasitic infection. Finally, the desirability of examining more than one stool specimen is recognized.

TABLE 2.—Incidence of oral and perianal parasites in a group of 539 Navy recruits

	Number	Per cent
Endamoeba gingivalis	104	19.2
Trichomonas tenax	12	2.2
TOTALS	116	21.4
Enterobius vermicularis	22	4.08

The incidence of oral protozoa and perianal pinworm incidence is presented in table 2. The group of 539 recruits examined includes 26 from the southeast who were trained at Great Lakes. It was not possible to attempt any correlation between incidence of oral amebae and trichomonads and oral health. Although the gingival ameba is more often found in cases of incipient to advanced pyorrhea, its presence in apparently normal mouths still permits some doubt as to its pathogenicity.

The 4 per cent incidence of pinworm infection is probably much too low since time permitted an average of only 2.4 examinations per man. Most investigators of enterobiasis agree that at least 6 examinations be made before a negative report is valid. The practicability of the scotch cellulose tape method for rapid processing of large groups of examinees was quite apparent. As Headlee (1951) points out, this method has the added advantage of greater reliability. It is interesting to note that pinworm eggs were not recovered in a double examination of every fecal specimen in this group. Among 496 stool specimens from the southeast group, a single pinworm infection was diagnosed from the fecal sample. In cases where as many as three perianal samples were obtained, 45 per cent of those diagnosed as positive were found after the first examination, 36 per cent after the second, and 18 per cent after the third examination.

Among the methods of concentrating cysts and ova, the zinc-sulfate-centrifugal floatation technic was the most effective of the three used. The recently developed MIF (merthiolate-iodine-formaldehyde) staining technic has definite advantages over other commonly used stains. Sapero (personal communication) further suggests a new combined stain-preservation technic which should prove most desirable for collection and preservation of fecal samples.

SUMMARY

A total of 1009 male Navy recruits was surveyed for incidence of intestinal parasites.

No significant difference was found in the incidence of protozoan parasites between a group of midwestern recruits and a group from the southeastern United States.

Helminth infections were found only in the recruits from southeastern areas.

A survey of oral protozoa and perianal pinworm infection was made on a group of 539 recruits.

The general incidence of parasitic infection was lower than that reported for the general population. Possible reasons for the differences are suggested.

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A Catalogue of the Protozoa and Helminths of North American Rodents. IV. Trematoda

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This is the last of four papers summarizing the host and geographical distribution records of the protozoa and helminths reported from North American rodents (order Rodentia). The organization and limitations of this part of the catalogue are the same as those outlined in Part I (Protozoa and Acanthocephala).

TREMATODA

1. *Agadomistomum* (apparent misspelling for *Agamodistomum*) sp.—*Ondatra zibethica* ssp.—Vt. (14).
2. *Agamodistomum norvegicum* Loewen, 1934 (metacercariae).—*Rattus norvegicus* [*Epimys norvegicus*—Kan. (49)].
3. *Alaria mustelae* Bosma, 1931.—*Ondatra zibethica* ssp.—Ont. (43), Minn. (68); *Peromyscus leucopus noveboracensis*—Mich. (13).
4. *Allassogonoporus marginalis* Olivier, 1938.—*Ondatra zibethica* ssp.—Mich. (64).
5. *Amphimerus pseudofelineus* (Ward, 1901) Barker, 1911.—*Ondatra z. zibethica*—Minn. (68) [*Fiber zibethicus*—Nebr. (6)].
6. *A. speciosus* (Stiles and Hassall, 1896) Barker, 1911.—*Rattus norvegicus*—D. C. (25).
7. *Amphistomum subtriquedrum* Rudolphi, 1814 [=*Stichorchis subtriquetrus* (Rudolphi, 1814) Fischoeder, 1901 (32) (26) (91)].—*Castor* sp.—Mich. (60); *C. canadensis* ssp.—Que. (99) (28), Ont. (28); *Ondatra z. zibethica* [*Fiber zibethicus*—(46)] (See Nos. 18, 62, 65, 89).
8. *Apophallus brevis* Ransom, 1911.—*Ondatra z. zibethica*—Minn. (68).
9. *A. donicus* (Skrjabin and Lindtrop, 1919) Price, 1931.—*Rattus norvegicus*—D. C. (74), Va. (72).
10. *Ascocotyle* (*Parascocotyle*) *diminuta* Stunkard and Haviland, 1924 [=*Ascocotyle* (*Phagicola*) *diminuta* (63)].—*Rattus norvegicus*—N. Y. (93).
11. *Brachylaima rauschi* McIntosh, 1950.—*Dicrostonyx groenlandicus rubricatus*—Alas. (56) (80); *Microtus miurus paneaki*—Alas. (80).
12. *B.* (*Postharmostomum*) *sexconvolutum* Miller, 1936 [=*Postharmostomum helicis* (Leidy, 1847) Robinson, 1949 (86) (97)]—*Peromyscus manisulatus* ssp.—Ohio (59) (See Nos. 15, 73, 75).
13. *B.* sp. (*rauschi ?*) of Rausch, 1952.—*Microtus pennsylvanicus terraenovae*—Newfoundland (80).
14. *Brachylaemus peromysci* Reynolds, 1938.—*Peromyscus l. leucopus*—Va. (83).
15. "brachylaemid" [=("?") *Postharmostomum helicis* (Leidy, 1847)].—*Mus* sp.—N. Y. (85); *Peromyscus leucopus*—N. Y. (85) (See Nos. 12, 75, 73).
16. *Catatropis filamentis* Barker, 1915 [=*Notocotylus filamentis* (Barker, 1915) Harwood, 1939].—*Ondatra zibethica* ssp.—Mich. (3), Ill. (48), Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See Nos. 17, 49).
17. *C. fimbriata* Barker, 1915 [=*Notocotylus filamentis* (Barker, 1915) (37)].—*Ondatra z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See Nos. 16, 49).
18. *Cladorchis* (*Stichorchis*) *subtriquetrus* (Rudolphi, 1814) Fischoeder, 1901 [=*Strichorchis subtriquetrus* (Rudolphi, 1814) Nasmark, 1937 (91)].—*Castor canadensis* ssp.—Ont. (44); *C. c. canadensis*—Ont. (19); *C.* sp.—Ont. (44); *Ondatra zibethica* ssp.—(8) (See Nos. 7, 62, 65, 89).
19. *Dicrocoelium dendriticum* (Rudolphi, 1819) Looss, 1899.—*Marmota monax rufescens*—N. Y. (50).
20. *Distoma cteniceps* Leidy [=*Echinostoma revolutum* (Froelich, 1802) Dietz, 1910 (8) (26)].—*Ondatra z. zibethica* [*Fiber zibethicus* (92)] (See Nos. 21, 25, 26, 28, 29).
21. *Distomum echinatum* (Zeder, 1803) Dietz, 1910 [=*Echinostoma revolutum* (Froelich)—(10) (26)].—*Ondatra z. zibethica* [*Fiber zibethicus* (46)] (See Nos. 20, 25, 26, 28, 29).
22. *Echinochasmus schwartzi* Price, 1931.—*Ondatra zibethica* ssp. Md. (71), Texas (22), Ont. (44); *O. z. rivalica*—La. (66) [*Ondatra rivalica*—La. (15)]; *O. z. macrodon*—Md. (67).
23. *Echinoparyphium contiguum* Barker and Bastron, 1915.—*Ondatra zibethica* ssp.—Mich. (3), Ont. (44); *O. z. zibethica*—Minn. (68) [*Fiber zibethicus*—Nebr. (7)].
24. *E. recurvatum* (Linstow, 1873) Dietz, 1909.—*Ondatra z. zibethica*—Maine (58), Minn. (68).

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* This work was started at the University of California, Los Angeles.

25. *Echinostoma revolutum* (Froelich, 1802) Dietz, 1910.—*Ondatra zibethica* ssp.—Mich., Minn. (68), Mass. (76) (77), Ill. (48) (95); *O. z. zibethica*—Maine (58), N. Y. (28); *Rattus norvegicus*—Mex. (101) (See Nos. 20, 21, 26, 28, 29).

26. *Echinostomum armigerum* Barker and Irvine, 1915 [=*Echinostoma revolutum* (Froelich) (10)].—*Ondatra zibethica* ssp.—Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See Nos. 20, 21, 25, 28, 29).

27. *E. callawayensis* Barker and Noll, 1915.—*Ondatra zibethica* ssp.—Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7)].

28. *E. coalitum* Barker and Beaver, 1915 [=*Echinostoma revolutum* (Froelich (10)].—*Ondatra zibethica* ssp.—Mich. (3), Ohio (78), Ont. (44); *O. z. zibethica*—Md. (41) [*Fiber zibethicus*—Nebr. (7)] (See Nos. 20, 21, 25, 26, 29).

29. *E. echinatum* Zeder, 1803 [=*Echinostoma revolutum* (Froelich) (10)].—*Ondatra zibethica zibethica* [*Fiber zibethicus* 46] (See Nos. 20, 21, 25, 26, 28).

30. *E.* sp.—*Ondatra zibethica* ssp.—Alba. (94); *O. z. osoyoosensis*—Colo. (5).

31. *Entosiphonus thompsoni* Sinitsin, 1931.—*Microtus p. pennsylvanicus*—Wisc. (82); *Peromyscus l. leucopus*—N. C. (34); *P. l. noveboracensis*—Md. (40).

32. *Euparyphium ochoterenai* Zerecero, 1943.—*Rattus norvegicus*—Mex. (101)

33. *Euryhelmis pacificus* Senger and Macy, 1952.—*Ondatra zibethica* ssp.—Ore. (88).

34. *Eurytrema komareki* McIntosh, 1939.—*Peromyscus g. gossypinus*—Ga. (55).

35. *Fibricola caballeroi* Zerecero, 1943.—*Rattus norvegicus*—Mex. (101).

36. *F. cratera* (Barker and Noll, 1915) Dubois, 1938.—*Rattus norvegicus*—Wisc. (87), Minn. (68) (See No. 38).

37. *F. nana* Rausch, 1946.—*Sciurus hudsonicus* ssp.—Mich. (23); *Tamiasciurus hudsonicus* ssp.—Mich. (81).

38. *Hemistomum craterum* Barker and Noll, 1915 [=*Fibricola cratera* (Barker, 1915 (27)].—*Ondatra zibethica* ssp.—Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See No. 36).

39. *Heterechinostomum magniovatum* Stunkard and Haviland, 1924.—*Rattus norvegicus*—N. Y. (93).

40. *Levinseniella brachysoma* (Creplin, 1878) Stiles and Hassall, 1901.—*Ondatra z. zibethica*—Minn. (68).

41. *Mediogonimus ovilacus* Woodhead and Malewitz, 1936.—*Microtus pennsylvanicus pennsylvanicus*—Mich. (82) (100); *Ondatra z. zibethica*—Minn. (68).

42. *Metorchis* sp.—(See No. 61).

43. *Monostomum affini* Leidy, 1858 [=*Notocotyle* (?) *affini* (Leidy, 1858) Barker, 1916 (8); =*nomen nudum* (71)].—*Ondatra z. zibethica* [*Fiber zibethicus* (45)] (See No. 47).

44. *Monostoma* sp., U. S. N. M. 5769 and 5770 [=*Q. quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939 (35) (37)].—*Ondatra z. zibethica* [*Fiber zibethicus*—Md. (92)] (See Nos. 48, 50, 51, 53, 80).

45. *M.* sp., U. S. N. M. 5773 [=*Quinqueserialis hassalli* (McIntosh and McIntosh, 1934) Harwood, 1939 (35) (37) (57)].—*Microtus p. pennsylvanicus* [*Arvicola riparus*—Md. (92)] (See Nos. 52, 79).

46. *Neodiplostomum* sp.—*Ondatra z. zibethica*—Minn. (68).

47. *Notocotyle* (?) *affini* (Leidy, 1858) Barker, 1916.—(See No. 43).

48. *N. quinqueseriale* Barker and Laughlin, 1911 [=*Q. quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939 (35) (37)].—*Ondatra zibethica* ssp.—Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7) (9)]; *O. z. osoyoosensis*—Colo. (5) (See Nos. 50, 51, 53, 44, 80).

49. *Notocotylus filamentis* (Barker, 1915) Harwood, 1939.—*Ondatra zibethica* ssp.—Mich. (37); *O. z. zibethica*—Maine (58) (See Nos. 16, 17).

50. *N. quinqueserialis* (Barker and Laughlin, 1911) Harrah, 1922 [=*Q. quinqueserialis* (Barker and Laughlin, 1911) (37)].—*Microtus pennsylvanicus* ssp.—N. Y. (29), *Mich.* (68); *Ondatra zibethica* ssp.—Mich. (3), Ohio (78); *O. z. zibethica*—N. Y. (29), Mich., Minn., (68) [*Fiber zibethicus*—Wash. (35)]; *Synaptomys c. cooperi*—Mich. (68); *Zapus hudsonius* ssp.—Mich. (68) (See Nos. 44, 48, 51, 53, 80).

51. *N. urbanensis* (Cort, 1914) Harrah, 1922 [=*Q. quinqueserialis* (Barker and Laughlin, 1911) (37)].—*Ondatra zibethica occipitalis*—Ore. (84); *O. z. zibethica*—N. Y. (29), Mich., Minn. (68) (See Nos. 44, 48, 50, 53, 80).

52. *N. hassalli* McIntosh and McIntosh, 1934 [=*Q. hassalli* (McIntosh and McIntosh, 1934) Harwood, 1939].—*Microtus p. pennsylvanicus*—Md., Va. (57) (See Nos. 45, 79).

53. *N. hassalli* McIntosh and McIntosh of Erickson, 1938 [redetermined as *N. quinqueserialis* by (68)].—*Zapus h. hudsonius*—Mich. (31) (See Nos. 44, 48, 50, 51, 80).

54. *N.* sp. (*hassalli* ?) [=*Quinqueserialis* sp. (*hassalli* ?)].—*Zapus h. hudsonius*—Mich. (30) (See No. 81)

55. *N.* sp.—*Ondatra zibethica* ssp.—N. Y. (14).

56. *Nudacotyle novicia* Barker, 1916.—*Microtus pennsylvanicus* ssp.—Iowa (2); *M. p. pennsylvanicus*—Mich. (4); *Ondatra zibethica* ssp.—Mich. (3), Texas (22), Minn. (8), Ont. (44); *O. z. rivalica*—La. (66); *O. z. zibethica*—Maine (58), Minn., Mich. (68); *O. z. macrodon*—Dela., N. J., Md. (68).

57. *Oligorchis nonarmatus* Neiland, 1952.—*Tamiasciurus d. douglasii*—Ore. (62).

58. *Opisthorchis tonkae* Wallace and Penner, 1939.—*Ondatra zibethica* ssp.—Minn. (98); *O. z. zibethica*—N. Y. (29), Minn. (68).

59. *Paragonimus rudis* (Diesing, 1850) Braun, 1899.—*Ondatra zibethica* ssp.—U. S. (17).

60. *P. kellicotti* Ward, 1908.—*Ondatra zibethica* ssp.—Mich. (1), Minn. (68).

61. *Parametorchis* sp. [=*Metorchis* sp. (20)].—*Ondatra zibethica macrodon*—Md. (90) (See No. 42).

62. *Paramphistomum castori* Kofoid and Park, 1937 [=*Stichorchis subtriquetrus* (Rudolphi, 1814) Nasmark, 1937 (32)].—*Castor canadensis baileyi*—Nev. (39) (See Nos. 7, 18, 65, 89).

63. *Paramonostomum echinum* Harrah, 1922.—*Ondatra z. zibethica* [*Fiber zibethicus*—Colo. (35)].

64. *P. pseudalveatum* Price, 1931.—*Ondatra zibethica* ssp.—Md. (71) (36); *O. z. rivalica*—La. (66).
65. *Paramphistome* sp. (miracidium) [=(?) *Stichorchis subtriquetrus* (Rudolphi) (12)].—*Castor canadensis carolinensis*—La. (11) (See Nos. 7, 18, 62, 89).
66. *Phagicola lageniformis* Chandler, 1941.—*Ondatra zibethica* ssp.—Texas (22).
67. *P. nana* (Ransom, 1921) Price, 1932.—*Ondatra zibethica rivalica* [*Ondatra rivalica*—La. (15)].
68. *Plagiorchis maculosus* (Rudolphi, 1802) Braun, 1902.—*Ondatra z. zibethica*—Minn. (68).
69. *P. microcanthos* Macy, 1931.—*Ondatra z. zibethica*—Minn. (68).
70. *P. muris* (Tanabe, 1922).—*Ondatra z. zibethica*—Minn. (68).
71. *P. proximus* Barker, 1915.—*Citellus richardsonii* ssp.—Man. (81); *Ondatra zibethica* ssp.—Mass. (77), Mich. (3), Ohio (78), Ont. (44); *O. z. osoyoosensis*—Colo. (5); *O. z. zibethica*—Maine (58), N. Y. (29) [*Fiber zibethicus*—Nebr. (7)].
72. *P.* sp.—*Clethrionomys rutilus dawsoni*—Alas. (80).
73. *Postharmostomum helicis* (Leidy, 1847) Robinson, 1949.—(See Nos. 12, 15, 75).
74. *P. novehoracensis* McIntosh, 1937.—*Tamias striatus lysteri*—N. Y. (53).
75. *P. laruei* McIntosh, 1934 [=*P. helicis* (Leidy, 1847) Robinson, 1949 (86)].—*Tamias striatus lysteri*—Mich. (51) (See Nos. 12, 15, 73).
76. *Pseudodiscus zibethicus* (Barker and East, 1915) Fukui, 1929.—*Ondatra zibethica* ssp.—Mich. (3); *O. z. zibethica*—Maine (58), N. Y. (29), Mich., Minn. (68) (See No. 93).
77. *Psilostomum ondatrae* Price, 1931 [=*Ribeiroia ondatrae* (Price, 1931) Price, 1942].—*Ondatra zibethica* ssp.—Ont. (44) (71), Minn. (68) (See No. 84).
78. *Quinqueserialis floridensis* Rausch, 1952.—*Neofiber alleni nigrescens*—Fla. (79).
79. *Q. hassalli* (McIntosh and McIntosh, 1934) Harwood, 1939.—*Microtus montanus nanus*—Wyo. (42); *M. ochrogaster*—No. Cent. States (82); *M. pennsylvanicus modestus*—Wyo. (42); *M. p. pennsylvanicus*—Md., Va. (37), No. Cent. States (82) (See Nos. 45, 52).
80. *Q. quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939.—*Microtus oeconomus macfarlani*—Alas. (80); *M. pennsylvanicus drummondi*—Alas. (80); *M. p. pennsylvanicus*—Minn. (37); *Ondatra zibethica* ssp.—Iowa, Mont., Md. (37); *O. z. zibethica*—Maine (58), Wisc. (82) (See Nos. 44, 48, 50, 53, 51).
81. *Q.* sp. (*hassalli* ?).—See No. 54).
82. *Q.* sp. of Rausch and Tiner, 1949 [previously reported as *Q. hassalli* by (81)].—*Marmota monax* ssp.—Wisc. (82).
83. *Renifer ellipticus* Pratt, 1903.—*Castor canadensis*—*Pa.* *(21).
84. *Ribeiroia ondatrae* (Price, 1931) Price, 1942.—(See No. 77)
85. *Scaphiostomum pancreaticum* McIntosh, 1934.—*Peromyscus g. gossypinus*—Ga. (52); *Tamias striatus lysteri*—Mich. (51); *T. striatus (griseus ?)*—Wisc. (81).
86. *Schistosomatium douthitti* (Cort, 1914) Price, 1929.—*Microtus pennsylvanicus* ssp.—Mich. (75); *M. p. pennsylvanicus*—Mich. (75); *Ondatra zibethica* ssp.—Mich. (3) (67); "rat" (*Rattus norvegicus* ?)—Minn. (70).
87. *S.* sp. (*douthitti* ?).—*Microtus* sp.—Minn. (70).
88. *Stephanoproaroides lawi* Price, 1931.—*Castor canadensis* ssp.—Minn (32), Ont. (73).
89. *Stichorchis subtriquetrus* (Rudolphi, 1814) Nasmark, 1937.—*Castor* sp.—Pa. (61), Ore. (89); *Castor canadensis* ssp.—Minn (32), Colo. (65); *C. c. carolinensis*—La. (12); *C. c. mexicanus*—Mex. (18); *Ondatra zibethica* ssp.—La. (11) (See Nos. 7, 18, 62, 65).
90. "trematode."—*Castor c. canadensis*—N. Y. *(38); *Ondatra z. zibethica*—Ont. (43) [*Fiber zibethicus*—Mass. (95)]; *Sciurus c. carolinensis*—Ohio (24).
91. *Urotrema scabridum* Braun, 1900.—(See No. 92).
92. *U. schillingeri* Price, 1931 [=*U. scabridum* Braun (16)].—*Ondatra zibethica* ssp.—Md. (69) (71) (See No. 91).
93. *Wardius zibethicus* Barker and East, 1915 [=*Pseudodiscus zibethicus* (Barker and East, 1915) Fukui, 1929 (33)]; *Ondatra zibethica* ssp.—Ohio (78), Ont. (44); *O. z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See No. 76).

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HOST-INDEX TO PART III (NEMATODA) AND PART IV (TREMATODA)

(T=Trematoda; N=Nematoda. Numbers refer to the numbers preceding the parasite names listed under these two categories.)

family ERETIZONTIDAE

Genus *Erithizon* F. Cuvier (porcupines)
E. dorsatum ssp.: N-35, 36, 38, 40, 41, 42, 50, 94, 115, 116, 120, 186, 216.
E. d. dorsatum: N-36, 52, 92, 96, 168, 218.
E. epixanthum ssp.: N-115, 215, 216.

family CASTORIDAE

Genus *Castor* Linnaeus (beavers)
C. sp.: T-7, 18, 89; N-23, 48, 49, 152, 182.
C. canadensis ssp.: T-7, 18, 83, 88, 89; N-23, 33, 48, 182.
C. c. baileyi: T-18, 62.
C. c. canadensis: T-18, 90; N-16, 50, 183.
C. c. carolinensis: T-65, 89.
C. c. mexicanus: T-89.

family CRICETIDAE

Genus *Clethrionomys* Tilesius (red-backed mice)
C. sp.: N-86.
C. gapperi ssp.: N-103.
C. g. gapperi: N-116, 176.
C. rutilus dawsoni: T-72; N-149.

Genus *Dicrostonyx* Gloger (collared-lemmings)
D. sp.: N-173.
D. groenlandicus rubricatus: T-11; N-58, 173.
D. hudsonius: N-58.

Genus *Lemmus* Link (lemmings)
L. sp.: N-173.
L. trimucronatus alascensis: N-107.

Genus *Microtus* Schrank (meadow-mice)
M. sp.: T-87; N-86, 176.
M. longicaudus ssp.: N-143, 176.
M. l. littoralis: N-105.
M. l. mordax: N-176.
M. miurus paneaki: T-11; N-146.
M. montanus ssp.: N-176.
M. m. nanus: T-79; N-57, 106.
M. mordax ssp.: N-119.
M. ochrogaster: T-79; N-76, 176, 211.
M. oeconomus innuitus: N-146.
M. o. macfarlani: T-80.
M. pennsylvanicus ssp.: T-50, 56, 86; N-78, 101, 105.
M. p. drummondi: T-80; N-176.
M. p. modestus: T-79; N-176.
M. p. pennsylvanicus: T-31, 41, 45, 52, 56, 79, 80, 86; N-13, 34, 78, 86, 107, 119, 176, 208.
M. p. terraenovae: T-13.
M. richardsonii macropus: N-57, 106, 108, 176, 208.

Genus *Neofiber* True (round-tailed muskrats)
N. alleni nigrescens: T-78.

Genus *Neotoma* Say and Ord (wood-rats)
N. albigula ssp.: N-201.
N. a. albigula: N-93.
N. a. melanura: N-93.
N. cinerea rupicola: N-98, 119.

N. desertorum: N-98.
N. floridana baileyi: N-98, 119.
N. f. osagensis: N-13, 81, 206.
N. fuscipes ssp.: N-207.
N. f. macrotis: N-100.
N. lepida intermedia: N-100.
N. magister: N-149.
N. mexicana fallax: N-98, 116.
N. micropus ssp.: N-74, 93.

Genus *Ondatra* Link (muskrats)
O. zibethica ssp.: T-1, 3, 4, 16, 18, 22, 23, 25, 26, 28, 49, 55, 86, 89, 92; N-1, 4, 6, 7, 16, 17, 20, 39, 64, 71, 78, 105, 147, 164, 192, 208.
O. z. cinnamomina: T-27, 33, 38, 48, 58, 59, 60, 64, 66, 71, 76, 77, 80, 93; N-208.
O. z. macrodon: T-22, 56, 61; N-45, 208.
O. z. occipitalis: T-51; N-199.
O. z. ocoyooensis: T-30, 48, 71; N-208.
O. z. rivalica: T-22, 56, 64, 67; N-16, 75, 123, 129, 151.
O. z. zibethica: T-5, 7, 8, 16, 17, 20, 21, 23, 24, 25, 26, 28, 29, 38, 40, 41, 43, 44, 46, 48, 50, 51, 56, 58, 63, 68, 69, 70, 71, 76, 80, 90, 93; N-16, 20, 32, 39, 50, 55, 195, 208.

Genus *Onychomys* Baird (grasshopper-mice)
O. leucogaster ssp.: N-116, 148.
O. torridus ssp.: N-133.

Genus *Oryzomys* Baird (rice-rats)
O. palustris ssp.: N-84.
O. p. palustris: N-147.

Genus *Ototylomys* Merriam
O. phyllotis phyllotis: N-176.

Genus *Peromyscus* Glober (white-footed mice)
P. gossypinus gossypinus: T-34, 85; N-139.
P. g. megacephalus: N-139.
P. leucopus ssp.: T-15; N-84, 93, 148.
P. l. leucopus: T-14, 31; N-112, 143, 177.
P. l. noveboracensis: T-3, 31; N-9, 14, 149, 179, 181.
P. maniculatus ssp.: T-12; N-76, 143, 176.
P. m. bairdii: N-14, 143.
P. m. gracilis: N-9, 12, 179.
P. m. nebrascensis: N-76.
P. m. osgoodi: N-55.
P. nasutus: N-116.

Genus *Pitymys* McMurtie (pine-mice)
P. pinetorum pinetorum: N-119.

Genus *Reithrodontomys* Giglioti (harvest-mice)
R. megalotis ssp.: N-176.

Genus *Sigmodon* Say and Ord (cotton-rats)
S. sp.: N-75, 166.
S. hispidus ssp.: N-16, 71, 73, 75, 84, 93, 95, 97, 123, 127, 130, 167, 196, 212.
S. h. hispidus: N-55, 75, 84, 85, 127, 131, 166, 190.
S. h. littoralis: N-71, 125.
S. h. texianus: N-71, 134, 147, 166.
S. melanotis: N-71.

Genus *Synaptomys* Baird (bog-lemmings)
C. cooperi cooperi: T-50.

family GEOMYIDAE

Genus *Cratogeomys* Merriam (pocket-gophers)
C. merriami: N-77.

Genus *Geomys* Rafinesque (Eastern pocket-gophers)
G. sp.: N-84.
G. breviceps ssp.: N-84, 135.
G. b. breviceps: N-134.

Genus *Thomomys* Wied (Western pocket-gophers)
T. bottae bottae: N-202.
T. fossor: N-60, 64, 84, 111, 141, 202.
T. monticola ssp.: N-211.

family HETEROMYIDAE

Genus *Dipodomys* Gray (kangaroo-rats)
D. sp.: N-144.
D. merriami ssp.: N-205a, 217.
D. m. merriami: N-111.
D. ordii ssp.: N-205a.

Genus *Perognathus* Wied (kangaroo-mice)
P. baileyi ssp.: N-205a, 217.
P. californicus ssp.: N-210.
P. c. californicus: N-209.
P. flavus ssp.: N-205a.
P. intermedius ssp.: N-205a, 217.
P. penicillatus ssp.: N-209.
P. p. pricei: N-93, 133, 140, 205b, 217.

family MURIDAE

Genus *Mus* Linnaeus (house-mice)
M. musculus: N-10, 11, 16, 64, 66, 80, 104, 110, 114, 116, 117, 137, 138, 155, 176, 184.
M. m. "albus": N-10, 176, 184.

Genus *Rattus* G. Fischer (house-rats)
R. sp.: N-82.
R. norvegicus: T-2, 6, 9, 10, 25, 32, 35, 36, 39; N-16, 19, 22,

47, 53, 54, 59, 60, 63, 64, 66, 67, 85, 87, 93, 110, 116, 127, 136, 137, 138, 162, 163, 169, 176, 184, 185, 188, 189, 191, 206.
R. n. "albus": N-85, 138, 176, 189.
R. rattus: N-66, 116, 137, 176, 184, 189.
"rat" (*R. norvegicus* ?): T-86; N-66, 176, 184.

family SCIURIDAE

Genus *Citellus* Oken (ground-squirrels)
C. armatus: N-26, 174.
C. beecheyi ssp.; N-2, 91, 180, 200.
C. columbianus ssp.: N-27.
C. franklinii: N-15, 26, 128, 129, 142, 171.
C. lateralis ssp.: N-118.
C. leucurus cinnamomeus: N-118.
C. l. leucurus: N-118.
C. parryi barrowensis: N-3.
C. mexicanus ssp.: N-93.
C. richardsonii ssp.: T-71; N-16, 26, 51, 111, 129, 157, 159, 203, 213.
C. tridecemlineatus ssp.: N-128, 142, 157, 184.
C. t. tridecemlineatus: N-129, 142, 157.
C. t. pallidus: N-111, 156.
C. variegatus grammurus: N-205a.
C. v. variegatus: N-122.

Genus *Cynomys* Rafinesque (prairie-dogs)
C. sp.: N-65.
C. ludovicianus ssp.: N-64, 65, 123, 156, 187.
C. l. arizonensis: N-198.

Genus *Eutamias* Troussart (Western chipmunks)
E. amoenus ssp.: N-143, 176.
E. minimus ssp.: N-175.
E. m. jacksonii: N-26, 149.
E. m. operarius: N-68, 119.
E. quadrivittati ssp.: N-99, 119, 143, 214.

Genus *Glaucomys* Thomas (flying-squirrels)
G. sabrinus macrotis: N-26, 178.
G. volans volans: N-14, 26, 178.

Genus *Marmota* Blumenbach (woodchucks)
M. sp.: N-121.
M. caligata broweri: N-3.
M. monax ssp.: T-82; N-3, 25, 26, 113, 120.
M. m. canadensis: N-25, 30.
M. m. monax: N-3, 25, 29, 65, 113, 192, 199.
M. m. ochracea: N-5.
M. m. rufescens: T-19; N-26, 111.

Genus *Sciurus* Linnaeus (tree-squirrels)
S. sp.: N-4.
S. aberti nimus: N-194.
S. carolinensis ssp.: N-13, 62, 69, 88, 167.
S. c. carolinensis: T-90; N-4, 22, 26, 29, 56, 79, 111, 132, 150, 165.
S. c. hypophaeus: N-26, 199.
S. c. leucotus: N-13, 14, 22, 26, 56, 129, 145, 167, 192.
S. hudsonicus ssp.: T-37; N-8, 26.
S. niger ssp.: N-148.
S. n. bryanti: N-56, 61, 119, 165.
S. n. neglectus: N-26.
S. n. niger: N-13, 126.
S. n. rufiventer: N-2, 4, 6, 7, 13, 22, 26, 46, 56, 69, 89, 90, 149, 150, 165, 167, 192, 199.

Genus *Tamias* Illiger (Eastern chipmunks)
T. striatus ssp.: N-21, 22, 26, 145, 158, 199, 204.
T. s. lysteri: T-74, 75, 84; N-111, 145, 158.
T. s. griseus: T-85; N-145.

Genus *Tamiasciurus* J. A. Allen (red-squirrels)
T. douglassi douglassi: T-57.
T. hudsonicus ssp.: T-37; N-6, 26, 56, 149, 167, 178.
T. h. hudsonicus: N-26.

family ZAPODIDAE

Genus *Napaeozapus* Preble (jumping mice)
N. insignis ssp.: N-31.

Genus *Zapus* Coues (jumping-mice)
Z. hudsonicus ssp.: T-50.
Z. h. hudsonicus: T-53, 54; N-160, 161, 170, 172.

"wild mouse": N-154.
"wild rat": N-176.

Studies on Monogenetic Trematodes. XVII. The Genus Dactylogyrus[1]

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The genus *Gyrodactylus* von Nordmann, 1832, included all described species of *Dactylogyrus* prior to 1850 when Diesing established the latter taxonomic category. Validity of this separation was confirmed by Bychowsky when he erected the subfamily Dactylogyrinae in 1933(a). The first mention of *Dactylogyrus* in North America was that of Hess (1928) who reported undetermined species from various hosts. His observations were only partially correct since sunfish and small- and large-mouth basses which Dactylogyrinae normally do not infest, were included with goldfish, carp, and "other fishes" as harboring these species. Hess (1930) more correctly referred to goldfish and carp since *Dactylogyrus anchoratus* (Dujardin, 1845) was recorded from Europe for the former host and *D. extensus*, the first valid species record for North America, was described from the latter host by Mueller and Van Cleave in 1932. North American work on dactylogyrids was resumed when Mueller (1936) reported *D. anchoratus* (Dujardin, 1845) from the gills of *Carassius auratus*. Mueller (1936) observed the preponderance of *Dactylogyrus* species in Europe as compared to North America and concluded this genus to be predominantly European. Subsequent investigation proved this conclusion false as later admitted by Mueller (1938).

Mizelle (1937) described *Dactylogyrus bychowskyi*, *D. bifurcatus* and *D. simplexus* nov. nom. from the blunt-nosed minnow (*Hyborhynchus notatus*) and added *D. atromaculatus* from the creek chub (*Semotilus atromaculatus*) in 1938. Mueller (1938) described 16 new species from various minnows and suckers (Appendix I). Thus it became increasingly clear that this genus was almost as well represented in North America as in Europe and Asia, collectively (see below). The chief reason that earlier American workers failed to discover members of this subfamily is that examinations were restricted principally to native game fishes with almost total exclusion of cyprinids which comprise the largest family of North American freshwater fishes.

In 1938 Price erected the problematical genus *Neodactylogyrus* on the basis of the presence of two supporting haptoral bars. Kimpel (1939) reported the description of 6 species in this generic category (Appendix I). Mizelle and Donahue (1944) described 3 species, *D. banghami*, *D. bullosus* and *D. pollex* from the common shiner (*Notropis cornutus*) and questioned the validity of the genus *Neodactylogyrus*. Sproston (1946) recognized *Neodactylogyrus*, *Dactylogyrus* and *Dogielius* (monotypic) as the three genera which consti-

[1] Contribution from the Department of Biology, University of Notre Dame, Notre Dame, Indiana.

tute the subfamily Dactylogyrinae. Thapar erected the genus *Paradactylogyrus* in 1948. Validity of the genera *Neodactylogyrus* and *Paradactylogyrus* are discussed in the present work on page 465.

In 1945 Mizelle and Regensberger recorded *Dactylogyrus eucalius* from the brook stickleback (*Eucalia inconstans*). Seamster (1948) published the descriptions of *D. parvicirrus* and *D. aureus* from the golden shiner (*Notemigonus crysoleucas auratus*). Finally, Mizelle and Klucka (1953) described *D. attenuatus, D. claviformis, D. distinctus, D. dubius, D. lineatus, D. pyriformis* and *D. vannus* from Wisconsin cyprinids. The 9 new forms described in the present work make a total of 50 species of *Dactylogyrus* for North America (Appendix I). Presently there are 64 previously described species of *Dactylogyrus* from Europe and Asia (Appendix II).

MATERIALS AND METHODS

The material studied in the present work was collected from British Columbia, and Ontario (Canada) in 1951 by Dr. R. V. Bangham of the Department of Zoology, Wooster College, Wooster, Ohio and from Oklahoma in 1952 by Dr. George A. Moore of the Department of Zoology, Oklahoma A. and M. College, Stillwater. The authors are grateful to these unselfish and cooperative zoologists.

The host material was frozen as recommended by Mizelle (1938a) and then preserved in 2-5% formalin. The gills were removed and placed in small vials about 1/2 to 2/3 full of tap water and shaken vigorously in order to free the worms from branchial tissue. The material was then transferred to Syracuse watch-glasses, and diluted and decanted until clear enough for reliable examination with a binocular dissectoscope.

Individual specimens were collected with a capillary pipette equipped with a rubber bulb and transferred to a depression in a drop of solidified glycerin-gelatin medium on a clean glass slide. A cover-glass which was placed thereon settled in place as the medium was melted with gentle heat. The slide was allowed to cool, the mounting medium solidified, the perimeter of the cover-glass was sealed with ringing varnish and a permanent mount was thus produced. All specimens recovered up to a maximum of 20 were used in the description of each species.

Measurements were made with a compound microscope and a calibrated ocular micrometer for 1) body length, 2) greatest body width, 3) haptor width, 4) haptor length, 5) length of anchors, 6) width of anchor bases, 7) length of haptoral bars, 8) length of cirrus, 9) length of accessory piece, 10) length of hooks, and 11) transverse diameter of pharynx. Curved structures were measured as a straight line extending between the two most distant points of the structure. Measurements of anchor length, for example, extend from the tip of the superficial root to the most distant point on the curved portion in the region of junction of the shaft and point. The width of the anchors is the greatest width of an anchor base. A mean measurement was calculated for three or more specimens and consists of an average derived from the measurements of the same structure in the different specimens measured. All measurements except those for body length and body width which were made with the aid of a low-power objective (10x), were accomplished with an oil-

immersion objective (95x). Measurements in quotation marks are those from an original description and are cited in a comparative manner for *D. banghami* Mizelle and Donahue, 1944.

DACTYLOGYRUS BANGHAMI Mizelle and Donahue, 1944

Figs. 1-13

Hosts and localities.—*Richardsonius balteatus* (Richardson), Marquette, Rosen, Lakelse, Surveyor's, Chemney, and Courtenay Lakes, St. George Creek, all British Columbia, Canada, *Couesius plumbeus dissimilis* (Girard), Middle River near Takla Lake, British Columbia, Canada. *Rhinichthys cataractae* (Valenciennes), Deep Creek, British Columbia, Canada. *Notropis cornutus* (Agassiz), Manitoulin River, Ontario, Canada. *N. volucellus buchanani* Meek and *N. lutrensis* (Baird and Girard), Lagoon Creek, Creek Co., Okla. *Hybognathus p. placita* Girard, *Notropis deliciosus missuriensis* (Cope), *N. girardi* (Hubbs and Ortenburger), *N. percobromus* (Cope), and *N. l. lutrensis* (Baird and Girard) all from Red Rock Creek, Pawnee Co., Okla.

Previously reported host and locality.—*Notropis cornutus* (Agassiz), Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944).

Specimens studied.—Twenty.

Location.—Gills.

Comparative description.—Relatively small dactylogyrid with a smooth, thin cuticle; length 0.362 mm (0.270-0.486 mm) "0.294 mm"; greatest body width 0.085 mm (0.054-0.126 mm) "0.078 mm" and generally in posterior body half. Eyespots four, usually of equal size; melanistic granules apparently of same type as those which comprise eyespots, usually present in vicinity of eyespots; spatial relationship of eyespots variable. Cephalic lobes 2 or 4 in number, head organs distinct; anterior cephalic margin cleft medially. Pharynx subspherical in dorsal outline and 0.021 mm (0.018-0.023 mm) "0.025 mm" in transverse diameter. Peduncle short and stout; haptor irregularly ovate in outline, width 0.047 mm (0.040-0.052 mm) "0.049 mm", length 0.048 mm (0.036-0.068 mm) "0.043" mm". Dorsal bar length 0.018 mm (0.016-0.020 mm) "0.020 mm", and variable in shape (figs. 1, 2). Vestigial ventral bar thin and bent medially in anterior direction (figs. 3-5), length 0.013 mm (0.012-0.014 mm) "0.014 mm" "crescentic," not observed in some specimens. Anchor bases bifurcate, shafts and points solid (figs. 8, 9), length 0.021 mm (0.020-0.023 mm) "0.020 mm", greatest width of base 0.013 mm (0.012-0.016 mm) "0.011 mm". Hooks fourteen in number, similar in shape, and normal in arrangement (Mizelle 1937);[2] hook lengths 0.015 mm (0.014-0.016 mm) "0.012-0.018 mm" (figs. 6, 7). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Copulatory complex as described by Mizelle and Donahue (1944, pl. 2, figs. 33-36) except for the presence of an enlarged tip on the basal projection of the cirrus (figs. 10, 11). Cirrus length 0.034 mm (0.027-0.041 mm) "0.036 mm". Accessory piece bifurcate as in original description (Mizelle and Donahue 1944, pl. 2, figs. 33, 35) but with a less refractile rod generally present on basal half of superior surface (fig. 12); length 0.022 mm (0.016-0.027 mm) "0.024 mm". Gonads obscured by dense vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Seminal vesicle well developed. Vagina present near mid-ventral surface toward right lower margin.

Dactylogyrus columbiensis n. sp.

Figs. 14-21

Host and locality.—*Ptychocheilus oregonensis* (Richardson), Kathlyn Lake, British Columbia, Canada.

Specimens studied.—One

Location.—Gills

Type specimen.—Type, U.S.N.M. Helm. Coll. no. 49457, Wash. D.C.

[2] The basic arrangement of haptoral hooks is the same in the Dactylogyrinae as in the Tetraonchinae

Description.—Relatively small dactylogyrid with a smooth thin cuticle; length 0.360 mm, greatest width 0.054 mm present in anterior body half. Eyespots four, approximately equal in size; distance between members of each pair subequal, accessory melanistic granules, apparently of same type as those which comprise eyespots, present in vicinity of eyespots, cephalic lobes conspicuous and 4 in number, head organs indistinct. Pharynx broadly ovate (transversely) in dorsal view and 0.020 mm in transverse diameter. Peduncle short, broad, and without constriction at junction with body and haptor; haptor subcircular in dorsal view; width 0.060 mm, length 0.060 mm. Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (fig. 19). Anchor wings conspicuous. Anchor length 0.038 mm, greatest width of base 0.013 mm. Dorsal bar (fig. 14) slightly bent posteriorly in middle and with rounded ends more accentuated than those of *D. tridactylus* n. sp. (figs. 111, 112); length 0.025 mm. Vestigial ventral bar distinct and tripartite (fig. 15); length 0.018 mm. Hooks fourteen in number, approximately equal in size and normal in arrangement (Mizelle 1937). Each hook consists of 1) an elongate-ovate solid base as long as or longer than 2) a slender solid shaft, and 3) a sickle-shaped termination and opposable piece (figs. 16, 17). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.022-0.023 mm. Gonads obscured by dense vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Seminal vesicle well developed; one large and 2 smaller prostates, each containing granular material. Vagina present near mid-ventral surface (fig. 18). Copulatory complex consisting of cirrus and accessory piece. Cirrus a thin, tapering, gently curved tube with an expanded base, length 0.018 mm (fig. 20). Accessory piece (fig. 21) more complicated than in *D. tridactylus* n. sp. (figs. 123, 124), length 0.018 mm.

The closest apparent relative of this form is *D. tridactylus* n. sp. which possesses similar haptoral armament and cirrus (figs. 14-17, 19, 20, 111-114, 116-122). Conspicuous differences between the two species are in the morphology of the accessory piece, vagina and ventral bar (figs. 15, 18, 21, 113-115, 123, 124).

Dactylogyrus hybognathus n. sp.

Figs. 22-34

Host and locality.—*Hybognathus p. placita* Girard, Red Rock Creek, Pawnee Co., Okla.

Specimens studied.—Eighteen

Location.—Gills

Type specimens.—Type and paratype, U.S.N.M. Helm. Coll. no. 49458, Wash., D.C.

Description.—Small dactylogyrid provided with a smooth, thin cuticle; length 0.245 mm (0.216-0.270 mm), greatest width 0.050 mm (0.045-0.054 mm) and usually near midlength. Eyespots four, usually equal in size, posterior pair occasionally larger, members of anterior pair always farther apart than those of posterior pair; accessory melanistic granules, apparently of same type as those which comprise eyespots, always present in vicinity of eyespots. Cephalic lobes two in number, anterior cephalic margin cleft medially. Head organs present but not conspicuous. Pharynx subcircular to broadly ovate (transversely) in dorsal view and 0.016 mm (0.012-0.020 mm) in transverse diameter. Peduncle variable in length-width relationship; haptor transversely ovate in dorsal view, width 0.034 mm (0.028-0.036 mm), length 0.029 mm (0.024-0.032 mm). Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (figs. 27, 28). Anchor wings well developed. Anchor length 0.019 mm (0.016-0.020 mm), greatest width of base 0.012 (0.011-0.013 mm). Dorsal bar bent medially in posterior direction (figs. 22, 23); length (0.013-0.014 mm). Vestigial ventral bar very small and only infrequently visible (figs. 24, 25), length 0.006 mm (0.005-0.007 mm). Hooks fourteen in number, approximately equal in size and normal in arrangement (Mizelle 1937). Each hook consists of 1) a small ovate solid base, 2) a slender, tapering solid shaft and 3) a sickle-shaped termination and opposable piece (figs. 29, 30). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.014 mm (0.013-0.016 mm). Vitellaria extending from posterior border of pharynx to anterior portion of peduncle. Ovary ovate in outline, situated in posterior body half, testis not observed. Seminal vesicle well developed. Vagina present

on right lateral margin, duct leading to vagina only occasionally visible. Copulatory complex composed of a cirrus and accessory piece. Cirrus a tapering, gently curved tube with an enlarged base, length 0.022 mm (0.020-0.023 mm) (figs. 31, 32). Accessory piece complicated (figs. 33, 34), length 0.011 mm (0.009-0.013 mm).

This species possesses a cirrus (figs. 31, 32) which remotely resembles that of *D. claviformis* Mizelle and Klucka (1953, fig. 49) but the accessory piece is morphologically unlike that of any other described member of the genus. The anchors (figs. 27, 28) are structurally similar to those of *D. perlus* Mueller (1938, pl. 3, fig. 18) while the hooks (figs. 29, 30) resemble those of *D. bullosus* Mizelle and Donahue (1944, pl. 2, figs. 28-30). The vestigial ventral bar (figs. 24, 25) of this form is unlike that of any North American species but somewhat resembles that of *D. difformis* Wagener (1857, pl. 15, fig. 3) and *D. mollis* Wedl (1857, pl. 4, fig. 51) of Europe.

Dactylogyrus moorei n. sp.

Figs. 47-54

Hosts and locality.—*Notropis deliciosus missuriensis* (Cope) and *Notropis l. lutrensis* (Baird and Girard), Red Rock Creek, Pawnee Co., Okla.

Specimens studied.—Five

Location.—Gills

Type specimens.—Type and 3 paratypes, U.S.N.M. Helm. Coll. no. 49460, Wash., D.C.

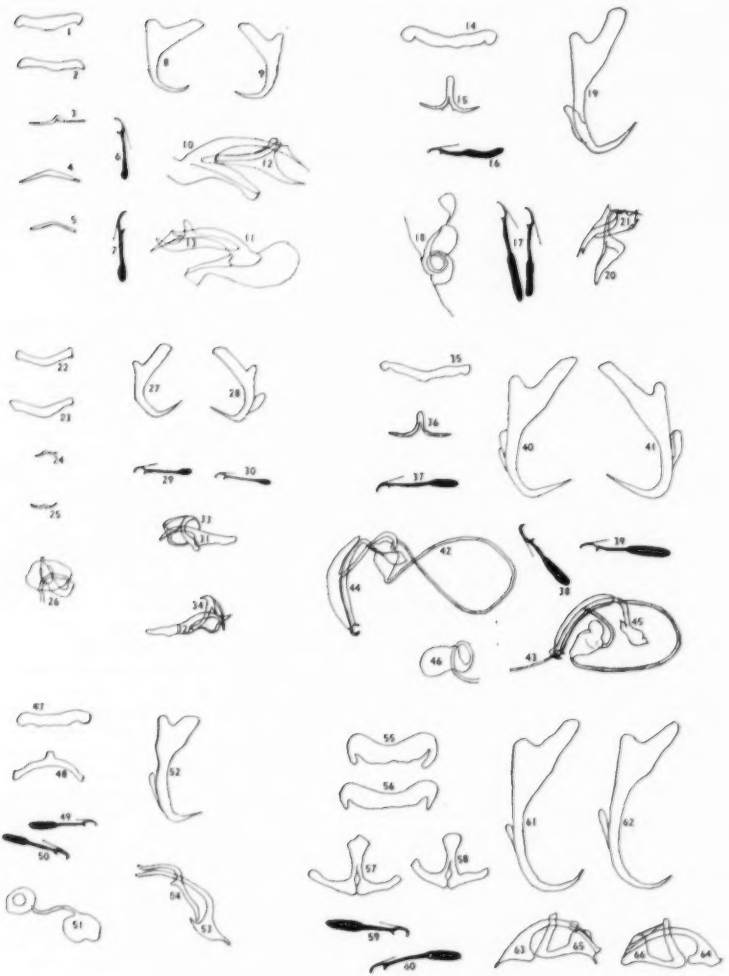
Description.—Relatively small dactylogyrid provided with a smooth, thin cuticle; length 0.246 mm (0.216-0.270 mm), greatest width 0.045 mm (0.036-0.054 mm) generally present in posterior body half. Eyespots four, approximately equal in size, distance between members of each pair variable, accessory melanistic granules, apparently of same type as those which comprise eyespots, generally dispersed in vicinity of eyespots. Cephalic lobes 2 in number; anterior cephalic region cleft medially. Head organs present but not conspicuous. Pharynx subcircular in dorsal view and 0.015 mm (0.014-0.018 mm) in transverse diameter. Peduncle short to moderately long; haptor ovate in dorsal view and longer than broad, width 0.034 mm (0.032-0.036 mm), length 0.036 mm. Anchors each composed of 1) a base with well-developed superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (fig. 52). Anchor wings present but poorly developed. Anchor length 0.027 mm, greatest width of base 0.010 mm (0.009-0.011 mm). Dorsal bar slightly bent posteriorly in the middle and gently curved on each end (fig. 47), length 0.022 mm. Vestigial ventral bar with median truncate projection on anterior border (fig. 48), length 0.018 mm. Hooks fourteen in number, approximately equal in size, and normal in arrangement (Mizelle 1937). Each hook consists of 1) a narrow solid base, 2) a slender solid shaft and 3) a sickle-shaped termination and opposable piece (figs. 49, 50). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.015 mm (0.014-0.018 mm). Ovary large and ovate; testis obscured by dense vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Seminal vesicle well developed. Vagina indistinct and situated on mid-ventral body surface near midlength of body proper (fig. 51). Copulatory complex consists of a cirrus and accessory piece. Cirrus varies from a long slender gently curved tube to a thicker tapering one with an expanded base (fig. 53), length 0.028 mm (0.025-0.030 mm). Accessory piece slender, articulated to base of cirrus and with prominent inferior projection near midlength (fig. 54), length 0.021 mm (0.018-0.023 mm).

The cirrus and accessory piece of this species (figs. 53, 54) resemble those of *D. urus* Mueller (1938, pl. 5, fig. 2) although the accessory piece in the present species has no characteristic distal extremity nor does the cirrus taper as greatly as in *D. urus*. An accessory piece similar to that of *D. moorei* is also present in *D. rubellus* Mueller (1938, pl. 5, fig. 6). The vestigial ventral bar of *D. moorei* is morphologically similar to that of *D. pyriformis* Mizelle and Klucka (1953, fig. 82) except that the median projection on this structure in the present species is truncate instead of pointed.

Dactylogyrus mylocheilus n. sp.

Figs. 55-66

Hosts and localities.—*Mylocheilus caurinus* (Richardson), Lakelse, Cuculz, Woods,



Figs. 1-66.[4] *D. banghami*—1, 2. Dorsal bars, 3-5. Ventral bars; 6, 7. Hooks; 8, 9. Anchors; 10, 11. Cirri; 12, 13. Accessory pieces. *D. columbiensis*—14. Dorsal bar; 15. Ventral bar; 16, 17. Hooks; 18. Vagina; 19. Anchor; 20. Cirrus. 21. Accessory piece. *D. hybognathus*—22, 23. Dorsal bars; 24, 25. Ventral bars; 26. Vagina; 27, 28. Anchors; 29, 30. Hooks; 31, 32. Cirri; 33, 34. Accessory pieces. *D. vancleavei*—35. Dorsal bar; 36. Ventral bar; 37-39. Hooks; 40, 41. Anchors; 42, 43. Cirri; 44, 45. Accessory pieces; 46. Vagina. *D. moorei*—47. Dorsal bar; 48. Ventral bar; 49, 50. Hooks; 51. Vagina; 52. Anchor; 53. Cirrus; 54. Accessory piece. *D. mylocheilus*—55, 56. Dorsal bars; 57, 58. Ventral bars; 59, 60. Hooks; 61, 62. Anchors; 63, 64. Cirri; 65, 66. Accessory pieces.

[4] All figures were drawn with the aid of a camera lucida.

and Vasseank Lakes, Ernie's Pothole, Sandy Point, all British Columbia, Canada. *Couesius plumbeus dissimilis* (Girard), Nelson, British Columbia, Canada.

Specimens studied.—Sixteen

Location.—Gills

Type specimens.—Types and 3 paratypes, U.S.N.M. Helm. Coll. no. 49461, Wash., D.C.

Description.—Relatively small dactylogyrid provided with a smooth, thin cuticle; length 0.414 mm (0.324-0.486), greatest width 0.079 mm (0.054-0.108 mm) usually present in posterior body half. Eyespots usually 4 (3 and 5 infrequently observed), usually equal in size; distance between members of each pair variable; accessory melanistic granules apparently of same type as those which comprise eyespots, always present in cephalic region. Cephalic lobes 2 or 4, anterior cephalic margin cleft medially. Head organs present but not conspicuous. Pharynx usually transversely (occasionally longitudinally) ovate, in dorsal view and 0.018 mm (0.016-0.022 mm) in transverse diameter. Peduncle short and stout; haptor transversely ovate in dorsal view, width 0.064 mm (0.060-0.072 mm), length 0.052 mm (0.040-0.060 mm). Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a relatively long solid shaft and 3) a solid point (figs. 61, 62). Anchor wings conspicuous. Anchor length 0.046 mm (0.045-0.049 mm), greatest width of base 0.015 mm (0.014-0.018 mm). Dorsal bar robust and yoke-shaped (figs. 55, 56), length 0.026 mm (0.023-0.029 mm). Vestigial ventral bar relatively large and inverted T-shaped, central area perforate (figs. 57, 58); length 0.022 mm (0.020-0.025 mm). Hooks fourteen in number, approximately equal in size, and normal in arrangement (Mizelle 1937). Each hook consists of 1) an elongate-ovate solid base as long as or longer than 2) a slender solid shaft, and 3) a sickle-shaped termination and opposaple piece (figs. 59, 60). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.023 mm (0.020-0.027 mm). Ovary not conspicuous, testis obscured by heavy development of vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Vagina not observed. Copulatory complex consisting of a cirrus and accessory piece. Cirrus a tapering tube with expanded base (figs. 63, 64)), length 0.024 mm (0.020-0.027 mm). Accessory piece conspicuously bent and provided with expanded terminal portion which partially encloses distal end of cirrus shaft (figs. 65, 66), length 0.015 mm (0.014-0.016 mm).

The perforated vestigial ventral bar and the yoke-shaped dorsal bar (figs. 55-58) resemble those of *D. scutatus* Mueller (1938, pl. 5, figs. 13-15) and *D. wunderi* Bychowsky 1933 (Nybelin, 1937, fig. 4). However, the copulatory complex, anchors and hooks (figs. 59-66) differ markedly from those of the above species which are considered the closest relatives of *D. mylocheilus.*

Dactylogyrus percobromus n. sp.

Figs. 67-82

Host and locality.—*Notropis percobromus* (Cope), Red Rock Creek, Pawnee Co., Okla.

Specimens studied.—Fourteen

Location.—Gills

Type specimens.—Type and 2 paratypes, U.S.N.M. Helm. Coll. no. 49462, Wash., D. C.

Description.—Small dactylogyrid provided with a smooth, thin cuticle; length 0.191 mm (0.144-0.288 mm), greatest width 0.038 mm (0.036-0.045 mm) usually near mid-length of body proper. Eyespots four, approximately of equal size, distance between members of each pair variable, few accessory melanistic granules, apparently of same type which comprise eyespots, present in vicinity of eyespots. Cephalic lobes prominent and four in number; anterior cephalic margin cleft medially. Head organs indistinct. Pharynx subcircular to broadly ovate (transversely) in dorsal view and 0.015 mm (0.014-0.016 mm) in transverse diameter. Peduncle short to approximately 1/5 body length; haptor ovate in dorsal view and broader than long, width 0.034 mm (0.032-0.036 mm), length 0.029 mm (0.028-0.032 mm). Anchors each composed of 1) a bifurcate base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (figs. 74, 75). Anchor wings indistinct. Anchor length 0.025 mm (0.023-0.027 mm, greatest width of base 0.010 mm (0.009-0.011 mm). Dorsal bar variable,

slightly bent posteriorly in midportion and with gently curved ends (figs. 67-69), length 0.015 mm (0.014-0.016 mm). Vestigial ventral bar with ends slightly curved posteriorly and a median triangular thickening (figs. 70-73); length 0.015 mm (0.014-0.016 mm). Hooks fourteen in number, approximately equal in size, and normal in arrangement (Mizelle 1937). Each hook consists of 1) an ovate solid base less than ½ as long as 2) a slender solid shaft, and 3) a sickle-shaped termination and opposable piece (figs. 76-78). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.015 mm (0.013-0.018 mm). Ovary pretesticular and ovate in outline. Vitellaria moderately diffuse, and extend as 2 bands from posterior border of pharynx to anterior portion of peduncle. Vagina not observed. Copulatory complex composed of a cirrus and accessory piece. Cirrus a tapered tube with expanded base (figs. 79, 80); length 0.018 mm (0.016-0.020 mm). Accessory piece (figs. 81, 82) Y-shaped somewhat as in *D. simplexus* (Mizelle) (1937, fig. 17), length 0.011 mm (0.011-0.013 mm).

This species is one of four similar North American forms and the present authors contend that these may be members of a complex. *D. simplexus* (Mizelle, 1937) nov. nom. (figs. 12-17) appears to be the closest relative of *D. percobromus*, however, *D. orchis* Mueller (1938, pl. 3, figs. 13-17) and *D. bifurcatus* Mizelle (1937, figs. 6-11) also show morphological affinities. The chief difference between *D. percobromus* and *D. simplexus* is expressed in the morphology of the accessory piece (figs. 81, 82; Mizelle 1937, fig. 17). *D. bifurcatus* is the most remote relative since the copulatory complex and size relationships differ markedly with those of the present species. The morphology of the haptoral armament of these four is very similar.

Dactylogyrus ptychocheilus n. sp.

Figs. 83-96

Host and localities.—*Ptychocheilus oregonensis* (Richardson), Lakelse and Kathlyn Lakes, One-mile Creek, all British Columbia, Canada.

Specimens studied.—Twenty

Location.—Gills

Type specimens.—Type and 3 paratypes, U.S.N.M. Helm. Coll. no. 49463, Wash., D.C.

Description.—Relatively small dactylogyrid provided with a smooth, thin cuticle; length 0.309 mm (0.234-0.414 mm), greatest width 0.072 mm (0.054-0.108 mm) usually present in posterior body half. Eyespots four, members of posterior pair usually larger than, but occasionally equal in size, to those of anterior pair, distance between members of each pair variable, accessory melanistic granules, apparently of same type which comprise eyespots, always dispersed in vicinity of eyespots. Cephalic lobes not observed; head organs indistinct. Pharynx broadly ovate (transversely) in dorsal view and 0.015 mm (0.012-0.016 mm) in transverse diameter. Peduncle short and stout and often same width as body proper and haptor; haptor ovate in dorsal view and broader than long, width 0.061 mm (0.048-0.072 mm), length 0.043 mm (0.040-0.052 mm). Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (figs. 88, 89). Anchor wings distinct. Anchor length 0.041 mm (0.040-0.045 mm), greatest width of base 0.015 mm (0.013-0.016 mm). Dorsal bar slightly bent posteriorly in midportion and with rounded ends (figs. 83-85); length 0.025 mm (0.022-0.027 mm). Vestigial ventral bar (fig. 86) similar to that of *D. vancleavei* (fig. 36) but with larger median portion, length 0.016 mm (0.014-0.018 mm). Hooks fourteen in number, approximately equal in size, and normal in arrangement (Mizelle 1937). Each hook consists of 1) an elongate-ovate solid base as long as or longer than 2) a tapering solid shaft, and 3) a sickle-shaped termination and opposable piece (figs. 90-92). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.023 mm (0.018-0.027 mm). Gonads obscured by dense vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Vagina conspicuous and present on ventral surface slightly on right of median line (fig. 87). Copulatory complex consists of a cirrus and accessory piece. Cirrus composed of an enlarged base and a curved tapering tube (figs. 93, 94), length 0.026 mm (0.023-0.029 mm). Accessory piece complicated (figs. 95, 96), length 0.015 mm (0.012-0.018 mm).

The accessory piece of *D. formosus* Kulwiec (1927, pl. 20, fig. 11) is structurally similar to that of *D. ptychocheilus* (figs. 95, 96). However, the cirrus in the present species

(figs. 93, 94) is radically different from that of *D. formosus* Kulwiec (1927, pl. 20, fig. 11). The anchors, hooks and bars of *D. formosus* Kulwiec (1927, pl. 20, figs. 7-10) are also different from these corresponding structures in *D. ptychocheilus* (figs. 83-86, 88-92). The ventral bar is similar to that of *D. parvus* Wegener (1909, fig. 10), *D. micracanthus* Nybelin (1937, fig. 14), and *D. borealis* Nybelin (1937, fig. 25). All other cuticularized structures of these species (Wegener 1909, figs. 9, 10; Nybelin 1937, figs. 12-14, 24, 25) however are morphologically different from those of *D. ptychocheilus* (figs. 83-85, 87-96).

Dactylogyrus richardsonius n. sp.

Figs. 97-110

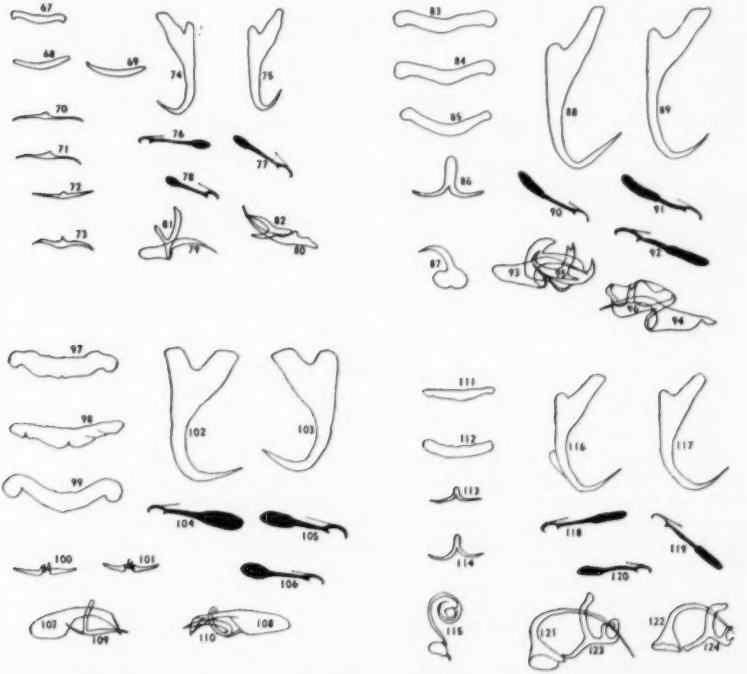
Host and locality.—*Richardsonius balteatus* (Richardson), Lakelse Lake, British Columbia, Canada.

Specimens studied.—Twenty

Location.—Gills

Type specimens.—Type and 3 paratypes, U.S.N.M. Helm. Coll. no. 49464, Wash., D.C.

Description.—Moderately large robust dactylogyrid provided with a smooth, thin



Figs. 67-124.[4] *D. percobromus*—67-69. Dorsal bars; 70-73. Ventral bars; 74, 75. Anchors; 76-78. Hooks; 79, 80. Cirri; 81, 82. Accessory pieces. *D. ptychocheilus*—83-85. Dorsal bars; 86. Ventral bar; 87. Vagina; 88, 89. Anchors; 90-92. Hooks; 93, 94. Cirri; 95, 96. Accessory pieces. *D. richardsonius*—97-99. Dorsal bars; 100, 101. Ventral bars; 102, 103. Anchors; 104-106. Hooks; 107, 108. Cirri; 109, 110. Accessory pieces. *D. tridactylus*—111, 112. Dorsal bars; 113, 114. Ventral bars; 115. Vagina; 116, 117. Anchors; 118-120. Hooks; 121, 122. Cirri; 123, 124. Accessory pieces.

[4] All figures were drawn with the aid of a camera lucida.

cuticle; length 0.558 mm (0.378-0.684 mm), greatest width 0.245 mm (0.198-0.306 mm) generally present in posterior body half. Eyespots four, members of posterior pair always larger and usually farther apart than members of anterior pair, accessory melanistic granules, apparently of same type as those which comprise eyespots, always dispersed in vicinity of eyespots. Cephalic lobes 2 in number and occasionally incipiently subdivided to form four; anterior cephalic margin with conspicuous median cleft. Head organs present but not conspicuous. Pharynx subcircular to broadly ovate (transversely) in dorsal view and 0.066 mm (0.056-0.072 mm) in transverse diameter. Peduncle short, broad; haptor sub-discoidal in dorsal view and broader than long, width 0.118 mm (0.100-0.140 mm), length 0.065 mm (0.044-0.080 mm). Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root slightly longer than deep root, 2) a solid shaft and 3) a solid point (figs. 102, 103). Anchor wings membranous, bag-like and variable in shape. Anchor length 0.032 mm (0.029-0.034 mm), greatest width of base 0.015 mm (0.014-0.016 mm). Dorsal bar variable, usually with rounded ends (figs. 97, 99); length 0.029 mm (0.025-0.032 mm). Vestigial ventral bar fragmented and usually visible; length 0.017 mm (0.014-0.020 mm) (figs. 100, 101). Hooks fourteen in number, approximately equal in size, and normal in arrangement (Mizelle 1937). Each hook consists of 1) a large solid base approximately as long as 2) a slender solid shaft, and 3) a sickle-shaped termination and opposable piece (figs. 104-106). Posteriorly projecting process on sickle-shaped termination, usually conspicuous, hook lengths 0.023 mm (0.022-0.025 mm). Ovary pretesticular and ovate in dorsal view; testis broadly overlaps ovary posteriorly. Vitellaria conspicuous and extend from posterior border of pharynx to anterior portion of peduncle. Vagina not observed. Copulatory complex composed of a cirrus and accessory piece. Cirrus relatively short and composed of a bulbous proximal portion and a tubular distal portion (figs. 107, 108); length 0.022 mm (0.020-0.023 mm). Accessory piece tripartite, one limb often obscured (figs. 109-110), length 0.011 mm (0.010-0.012 mm).

It is rather difficult to name the closest relative of *D. richardsonius* n. sp. The cirrus and accessory piece (figs. 107-110) remotely resemble those of *D. attenuatus* Mizelle and Klucka (1953, figs. 33-36), but the robust dorsal bar, anchors, hooks, fragmented ventral bar, and the relatively large size of *D. richardsonius* differ markedly from corresponding features in *D. attenuatus*.

Dactylogyrus tridactylus n. sp.

Figs. 111-124

Host and locality.—*Ptychocheilus oregonensis* (Richardson), Kathlyn Lake, British Columbia, Canada.

Specimens studied.—Two

Location.—Gills

Type specimens.—Type, U.S.N.M. Helm. Coll. no. 49465, Wash., D. C.

Description.—Relatively small dactylogyrid with a smooth, thin cuticle; length 0.270-0.306 mm, greatest width 0.072-0.090 mm generally present in posterior body half. Eyespots four, approximately equal in size, distance between members of each pair subequal; accessory melanistic granules apparently of same type as those which comprise eyespots, present in vicinity of eyespots. Cephalic lobes and head organs inconspicuous. Pharynx broadly ovate (transversely) in dorsal view and 0.020 mm in transverse diameter. Peduncle short and without constriction at junction of body and haptor; haptor transversely ovate in dorsal view, width 0.040-0.060 mm, length 0.032-0.036 mm. Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a solid shaft and 3) a solid point (figs. 116, 117). Anchor wings inconspicuous. Anchor length 0.031-0.032 mm, greatest width of base 0.013 mm. Dorsal bar variable in shape and with rounded ends (figs. 111, 112), length (0.022-0.023 mm). Vestigial ventral bar very small and observed with difficulty (figs. 113, 114), length 0.013 mm. Hooks fourteen in number, approximately equal in size and normal in arrangement (Mizelle 1937). Each hook consists of 1) an elongate-ovate solid base, 2) a slender solid shaft and 3) a sickle-shaped termination and opposable piece (figs. 118-120). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths (0.018-0.023 mm). Gonads obscured by dense vitellaria which extend from posterior border of pharynx to anterior portion of peduncle. Seminal vesicle well-developed. Vagina present near mid-

ventral surface (fig. 115). Copulatory complex consists of a cirrus and accessory piece. Cirrus a thin, tapering, gently curved tube with an expanded base (figs. 121, 122), length 0.020-0.022 mm. Accessory piece antler-like (figs. 123, 124), length 0.014-0.016 mm.

The closest known relative of *D. tridactylus* is *D. columbiensis* n. sp. described herein. The similarity of the haptoral armament (figs. 14-17, 19; 111-114, 116-120), vagina (figs. 18; 115) and cirrus (figs. 20; 121, 122) of these two species are striking. However the accessory piece of *D. tridactylus* (figs. 123, 124) is more similar to that of *D. apos* Mueller (1938, pl. 4, fig. 21) and *D. tenax* Mueller (1938, pl. 4 fig. 28).

Dactylogyrus vancleavei n. sp.

Figs. 35-46

Hosts and localities.—*Ptychocheilus oregonensis* (Richardson) Lakelse and Kathlyn Lakes, One-mile Creek, Middle River, all British Columbia, Canada. *Acrocheilus alutaceus* Agassiz & Pickering, Okanagan River, British Columbia, Canada.

Specimens studied.—Twenty

Location.—Gills

Type specimens.—Type and 2 paratypes. U.S.N.M. Helm. Coll. no. 49459, Wash., D.C.

Description.—Relatively small dactylogyrid provided with a smooth thin cuticle; length 0.367 mm (0.0198-0.432 mm), greatest width 0.092 mm (0.054-0.144 mm) usually near midlength of body proper. Eyespots four, usually equal in size; distance between members of each pair variable, accessory melanistic granules, apparently of same type as those which comprise eyespots, always dispersed in vicinity of eyespots and observed as far down as level of copulatory complex. Cephalic lobes conspicuous and four in number; head organs distinct. Pharynx subcircular to broadly ovate (transversely) in dorsal view and 0.022 mm (0.020-0.024 mm) in transverse diameter. Peduncle short and stout; haptor ovate in outline and broader than long, width 0.080 mm, length 0.060 mm (0.056-0.064 mm). Anchors each composed of 1) a base with well-defined superficial and deep roots, superficial root longer than deep root, 2) a relatively long solid shaft and 3) a solid point (figs. 40, 41). One and frequently two wings observed on anchor shaft. Anchor length 0.038 mm (0.036-0.040 mm), greatest width of base 0.016 mm (0.013-0.018 mm). Dorsal bar bent posteriorly at midlength and with slightly curved, rounded ends (fig. 35); length 0.022 mm (0.020-0.023 mm). Vestigial ventral bar small, not observed in some specimens, and composed of two limbs bent medially to unite to form an anterior projection (fig. 36); length 0.012 mm (0.011-0.013 mm). Hooks fourteen in number, approximately equal in size and normal in arrangement (Mizelle 1937). Each hook consists of 1) an elongate-ovate solid base approximately the same length as the 2) tapering solid shaft, and 3) a sickle-shaped termination and opposable piece (figs. 37-39). Posteriorly projecting process on sickle-shaped termination, usually conspicuous. Hook lengths 0.022 mm (0.018-0.025 mm). Vitellaria extend from posterior border of pharynx to anterior portion of peduncle. Ovary elongate-ovate, anterior to and overlapped dorso-posteriorly by the ovate testis. Seminal vesicle well developed. Vagina sinistral and lateroventral near body midlength (fig. 46). Copulatory complex composed of cirrus and accessory piece, unique. Cirrus a long uniform tube arising from a bulbous structure (prostate?) (figs. 42, 43) and projects through a tube-like accessory piece (figs. 44, 45), the proximal end of which is expanded whereas the distal end serves as a guide for the cirrus.

This form is readily distinguished from other species of *Dactylogyrus* by its characteristic copulatory complex. No close relatives have been described from North America. The cirrus (figs. 42, 43) resembles that of *D. zandti* Bychowsky (1933a, fig. 12), although the dorsal and vestigial ventral bars of *D. zandti* (fig. 11) differ markedly from those of *D. vancleavei* n. sp. (figs. 35, 36).

VALIDITY OF THE GENERA NEODACTYLOGYRUS AND PARADACTYLOGYRUS

Price (1938) erected the genus *Neodactylogyrus* to include all species of *Dactylogyrus* that have the two "Haptoral hooks (anchors) supported by 2 similar or dissimilar bars." The present authors wish to point out that the dorsal bar supports the bases of the two anchors (dorsal) in species assigned to this

category but that the ventral bar is not associated with these large hooks. This structure or *ventrales Chitinstück* is recognized as relict and apparently once supported the bases of a pair of ventral anchors as the ventral bar still does in the Tetraonchinae. *Neodactylogyrus* now has been recognized (Price 1938, Kimpel 1939, Sproston 1946), rejected (Mizelle and Donahue 1944), and ignored (Malevitskaja 1941, Mizelle and Klucka 1953, Mizelle and Webb 1953). Mizelle and Donahue based their rejection as follows: ". . . because the presence of the vestigial ventral bar required for assignment of species, thereto, is differentially developed, not always visible in fixed specimens, and results in unnecessary synonymy." The present authors agree that this structure is vestigial and also with Mayr et al. (1953) that such structures are not valid for sound taxonomic work. Reasons for the vestigial nature of this bar are 1) all species in the other subfamilies (except Bothitrematinae which includes a single species) of Dactylogyridae possess four anchors the bases of which are usually connected by bars indicating this to be the primitive condition; 2) since the ventral bar of *Dactylogyrus* is absent in some and present in other species, this structure apparently is more characteristic of one which is disappearing rather than one that is appearing; 3) the presence of a ventral bar without a pair of anchors is indicative of a previous condition in which the anchors were present; 4) bars in the Dactylogyridae are subject to much variation: they may be present as two individual structures each of which connects the bases of a given pair of anchors, fused to form one bar, one or both may be absent, or they may be fragmented to produce more than one structure for a given bar. The foregoing information convinces the present authors that *Neodactylogyrus* is not valid. The presence of a single spicular structure near the center of the haptor as described for the genus *Paradactylogyrus* Thapar (1948) is hardly sufficient for generic recognition and emphasizes the need for further study.

HOST SPECIFICITY OF DACTYLOGYRUS SPECIES

Although species of *Dactylogyrus* have been recovered from the gills of eleven families of fishes, they are primarily parasites of the Cyprinidae since 102 of the 113 species occur on species of this family of fishes (Appendix III). Bychowsky (1933), Nybelin (1937) and the present authors observed that *Dactylogyrus* species may be divided into four groups with regard to the number of host species they parasitize: those limited to one, two, three, and four or more host species. The present authors agree with Bychowsky and Nybelin that there is rather narrow host specificity in this genus since Table I shows that 61.95% of these parasites are found on a single host species, 24.78% on two host species, 5.31% on three host species, and 7.96% on four or more host species. Bychowsky (1933) concluded that host specificity of *Dactylogyrus* was so narrow that a given species would not parasitize two hosts incapable of producing hybrids. Nybelin (1937) supported this observation since he found on three cyprinid hybrids, only those Dactylogyrinae which parasitized the parents of the hybrids, fishes. Although the observations of Nybelin are doubtless correct, they are inconclusive since in the present work specimens of *Dactylogyrus banghami* Mizelle and Donahue (1944) have been recovered from 11 host species belonging to five genera (*Notropis, Hybognathus, Rhinichthys, Richardsonius* and *Couesius*) which in all probability would not hybridize (see p. 467). A similar phenomenon has been observed in the Old World species,

D. fallax Wagener, 1857, which is found on 9 host genera (p. 471). Moreover it is most improbable that members of Esocidae and Percidae would hybridize with cyprinids which harbor the same species of *Dactylogyrus* (*D. megastoma* Wagener, 1857; *D. amphibothrium* Wagener, 1857). In the light of this information it is apparent that Bychowsky's conclusions are questionable.

TABLE I.—Comparative specificity of *Dactylogyrus* species

Number of different host species parasitized	1	2	3	4	5	6	7–8	9	10	11
Number of North American *Dactylogyrus* species	40	8	1	0	0	0	0	0	0	1
Number of Old World *Dactylogyrus* species	30	20	5	3	1	3	0	1	0	0
Total species	70	28	6	3	1	3	0	1	0	1
Percent of species	61.95	24.78	5.31	2.65	0.88	2.65	0	0.88	0	0.88

APPENDICES

An attempt has been made in these appendices to bring up to date the information on the genus *Dactylogyrus* (as interpreted herein) contained in Sproston's monograph since this group has received considerable attention in North America since appearance of this work (1946). In addition to the description of nine new species, rejection of the genus *Neodactylogyrus* Price, 1938, and suggestion of further study before definite acceptance of the genus *Paradactylogyrus* Thapar, 1948, *D. simplex* Mizelle, 1937 (a homonym of *D. simplex* Bychowsky, 1936) is renamed *D. simplexus* nov. nom. and *D. elongatus* Jacob, 1940, is listed as a *nomen nudum* because the original referenced contains no description or illustrations. Other *nomina nuda* are listed at the end of Appendix III. Only valid host names are used as given by Sproston (1946).

No attempt has been made to question the validity of species known only to the authors through published descriptions.

Appendix I

NORTH AMERICAN DACTYLOGYRUS[3]

DACTYLOGYRUS ACUS Mueller, 1938.—*Notropis cornutus* (Agassiz), *Campostoma anomalum* (Agassiz), French Creek near Panama, N. Y. (Mueller 1938).

D. AMBLOPS Mueller, 1938.—*Hybopsis amblops* (Rafinesque), French Creek near Panama, N. Y. (Mueller 1938).

D. ANCHORATUS (Dujardin, 1845) Wagener, 1857.—*Carassius auratus* (Linnaeus), Ithaca, N. Y. (Mueller 1936). *Cyprinus carpio* Linnaeus, Twin Lakes, British Columbia, Canada (pr. auth.).

D. APOS Mueller, 1938.—*Hypentelium nigricans* (LeSueur), French Creek near Panama, N. Y. (Mueller 1938).

D. ATROMACULATUS Mizelle, 1938.—*Semotilus atromaculatus* (Mitchill), Embarrass River, Urbana, Ill. (Mizelle 1938); Embarrass River, Urbana, Ill., Drainage Ditch, Rantoul, Ill. (Kimpel 1939).

D. ATTENUATUS Mizelle and Klucka, 1953.—*Semotilus a. atromaculatus* (Mitchill), Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953).

D. AUREUS Seamster, 1948.—*Notemigonus crysoleucas auratus* (Rafinesque), Culwell's pond, Warner, Okla. (Seamster 1948). *Notemigonus c. crysoleucas* (Mitchill), Westhampton Lake, University of Richmond, Va. (Hargis 1953).

D. BANGHAMI Mizelle and Donahue, 1944.—*Notropis cornutus* (Agassiz), Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944); Manitoulin River, Ontario, Canada (pr. auth.). *Notropis volucellus buchanani* Meek, *Notropis l. lutren-*

3 Hosts and localities follow the names of respective species of *Dactylogyrus*.

sis (Baird and Girard), Lagoon Creek, Creek Co., Okla. (pr. auth.). *Hybognathus p. placita* Girard, *Notropis deliciosus missuriensis* (Cope), *Notropis girardi* (Hubbs and Ortenburger), *Notropis percobromus* (Cope), *Notropis l. lutrensis* (Baird and Girard), all Red Rock Creek, Pawnee Co., Okla. (pr. auth.). *Richardsonius balteatus* (Richardson), Marquette, Rosen, Lakelse, Surveyor's Chemney, and Courtenay Lakes, St. George Creek, all British Columbia, Canada (pr. auth.). *Rhinichthys cataractae* (Valenciennes), Deep Creek, British Columbia, Canada (pr. auth.). *Couesius plumbeus dissimilis* (Girard), Middle River near Takla Lake, British Columbia, Canada (pr. auth.).

D. BIFURCATUS Mizelle, 1937.—*Hyborhynchus notatus* (Rafinesque), Embarrass River and Drainage Ditch, Urbana, Ill. (Mizelle 1937).

D. BULBUS Mueller, 1938.—*Notropis cornutus* (Agassiz), Chautauqua Lake, N. Y. (Mueller 1938); Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944); Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953); Fish Creek, Bayfield Co., Wis. (Mizelle and Webb 1953).

D. BULLOSUS Mizelle and Donahue, 1944.—*Notropis cornutus* (Agassiz), Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944).

D. BYCHOWSKYI Mizelle, 1937.—*Hyborhynchus notatus* (Rafinesque), Embarrass River and Drainage Ditch, Urbana, Ill. (Mizelle 1937).

D. campostomus (Kimpel) n. comb.— *Campostoma anomalum* (Agassiz), Drainage Ditch near Rantoul, Ill. (Kimpel 1939).

D. CLAVIFORMIS Mizelle and Klucka, 1953.—*Semotilus a. atromaculatus* (Mitchill), Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953).

D. columbiensis n. sp.—*Ptychocheilus oregonensis* (Richardson), Kathlyn Lake, British Columbia, Canada (pr. auth.).

D. CONFUSUS Mueller, 1938.—*Clinostomus elongatus* (Kirtland), French Creek near Panama, N. Y. (Mueller 1938). *Notropis Umbratilis atripes* (Jordan), Embarrass, Kaskaskia, and Sangamon rivers, near Champaign, Ill.. (Kimpel 1939). *Notropis whipplii* (Girard), Embarrass, Kaskaskia, and Salt Fork rivers, near Urbana, Ill. (Kimpel 1939).

D. CORNUTUS Mueller, 1938.—*Notropis cornutus* (Agassiz), Chautauqua Lake, N. Y. (Mueller 1938); Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944); Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953); Fish Creek, Bayfield Co., Wis. (Mizelle and Webb 1953). *Erycimba buccata* Cope, Kaskaskia and Salt Fork rivers near Champaign, Ill. (Kimpel 1939).

D. DISTINCTUS Mizelle and Klucka, 1953.—*Notropis v. volucellus* (Cope), Trout Creek, Iowa Co., Wis. (Mizelle and Klucka 1953).

D. DUBIUS Mizelle and Klucka, 1953.—*Notropis cornutus frontalis* (Agassiz), Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953).

D. DUQUESNI Mueller, 1938.—*Moxostoma duquesni* (LeSueur), French Creek near Panama, N. Y. (Mueller 1938).

D. EUCALIUS Mizelle and Regensberger, 1945.—*Eucalia inconstans* (Kirtland), Brule Hatchery Pond near Brule, Wis. (Mizelle and Regensberger 1945).

D. EXTENSUS Mueller and Van Cleave. 1932.—*Cyprinus carpio* Linnaeus, Oneida Lake, N. Y. (Mueller and Van Cleave 1932, Mueller 1936); Lake Pepin, Wis. (Mizelle and Klucka 1953, Mizelle and Webb 1953); Clear Lake, Lake Co., Cal. (Haderlie 1953); Twin Lakes and Okanagan River near Oliver, British Columbia, Canada (pr. auth.).

D. FULCRUM Mueller, 1938.—Notropis cornutus (Agassiz), Chautauqua Lake, N. Y. (Mueller 1938).

D. hybognathus n. sp.—*Hybognathus p. placita* Girard, Red Rock Creek, Pawnee Co., Okla. (pr. auth.).

D. LINEATUS Mizelle and Klucka, 1953.—*Semotilus a. atromaculatus* (Mitchill), Fish Creek, Bayfield Co., Pine River, Clarence Co., Wis. (Mizelle and Klucka 1953).

D. MICROPHALLUS Mueller, 1938.—*Semotilus atromaculatus* (Mitchill), French Creek near Panama, N. Y. (Mueller 1938); Fish Creek, Bayfield Co. and Pine River, Clarence Co., Wis. (Mizelle and Klucka 1953).

D. moorei n. sp.—*Notropis l. lutrensis* (Baird and Girard), Red Rock Creek, Pawnee Co., Okla. (pr. auth.). *Notropis deliciosus missuriensis* (Cope), Red Rock Creek, Pawnee Co., Okla. (pr. auth.).

D. mylocheilus n. sp.—*Mylocheilus caurinus* (Richardson), Lakelse, Cuculz, Woods, and Vasseank lakes, Ernie's Pothole, Sandy Point, all British Columbia, Canada (pr.

auth.). *Couesius plumbeus dissimilis* (Girard), Nelson, British Columbia, Canada (pr. auth.).

D. ORCHIS Mueller, 1938.—*Notropis rubellus* (Agassiz), French Creek near Panama, N. Y. (Mueller 1938).

D. PARVICIRRUS Seamster, 1948.—*Notemigonus crysoleucas auratus* (Rafinesque), Culwell's pond, Warner, Okla. (Seamster 1948). *Notemigonus c. crysoleucas* (Mitchill), Westhampton Lake, University of Richmond, Va. (Hargis 1953).

D. percobromus n. sp.—*Notropis percobromus* (Cope), Red Rock Creek, Pawnee Co., Okla. (pr. auth.).

D. PERLUS Mueller, 1938.—*Notropis cornutus* (Agassiz), Chautauqua Lake, N. Y. (Mueller 1938); Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944).

D. phenacobius (Kimpel) n. comb.—*Phenacobius mirabilis* (Girard). Drainage Ditch, Rantoul, Ill. (Kimpel 1939).

D. PHOTOGENIS Mueller, 1938.—*Notropis photogenis* (Cope), French Creek near Panama, N. Y. (Mueller 1938).

D. POLLEX Mizelle and Donahue, 1944.—*Notropis cornutus* (Agassiz), Proulx Lake in Algonquin Park, Ontario, Canada (Mizelle and Donahue 1944).

D. ptychocheilus n. sp. *Ptychocheilus oregonensis* (Richardson), Kathlyn and Lakelse lakes, One-mile Creek, all British Columbia, Canada (pr. auth.).

D. PYRIFORMIS Mizelle and Klucka, 1953.—*Notropis cornutus frontalis* (Agassiz), Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953).

D. richardsonius n. sp.—*Richardsonius balteatus* (Richardson), Lakelse Lake, British Columbia, Canada (pr. auth.).

D. RUBELLUS Mueller, 1938.—*Notropis rubellus* (Agassiz), French Creek near Panama, N. Y. (Mueller 1938).

D. SCUTATUS Mueller, 1938—*Exoglossum maxillingua* (LeSueur) and *Parexoglossum laurae* Hubbs, French Creek, N. Y. (Mueller 1938).

D. semotilus (Kimpel) n. comb.—*Semotilus atromaculatus* (Mitchill), Embarrass River, Urbana, Ill. Drainage Ditch, Rantoul, Ill. (Kimpel 1939).

D. simplexus (Mizelle, 1937) nov. nom.—*Hyborhynchus notatus* (Rafinesque), Embarrass River and Drainage Ditch, Urbana, Ill. (Mizelle 1937).

D. superficialis (Kimpel) n. comb.—*Erycimba buccata* Cope, Kaskaskia and Salt Fork rivers near Champaign, Ill. (Kimpel 1939).

D. TENAX Mueller, 1938.—*Semotilus atromaculatus* (Mitchill), French Creek near Panama, N. Y. (Mueller 1938).

D. tridactylus n. sp.—*Ptychocheilus oregonensis* (Richardson), Kathlyn Lake, British Columbia, Canada (pr. auth.).

D. umbratilus (Kimpel) n. comb.—*Notropis umbratilis atripes* (Jordan), Embarrass, Kaskaskia and Sangamon rivers near Champaign, Ill. (Kimpel 1939).

D. URUS Mueller, 1938.—*Moxostoma anisurum* (Rafinesque), French Creek near Panama, N. Y. (Mueller 1938).

D. vancleavei n. sp.—*Ptychocheilus oregonensis* (Richardson), Kathlyn and Lakelse lakes, One-mile Creek, Middle River, all British Columbia, Canada (pr. auth.). *Acrocheilus alutaceus* Agassiz and Pickering, Okanagan River, British Columbia, Canada (pr. auth.).

D. VANNUS Mizelle and Klucka, 1953.—*Notropis cornutus frontalis* (Agassiz), Fish Creek, Bayfield Co., Wis. (Mizelle and Klucka 1953).

D. whipplius (Kimpel) n. comb.—*Notropis whipplii* (Girard), Embarrass, Kaskaskia, and Salt Fork rivers, near Urbana, Ill. (Kimpel 1939).

Appendix II

OLD WORLD DACTYLOGYRUS

DACTYLOGYRUS AFFINIS Bychowsky, 1933.—*Barbus brachycephalus* Kessler, Caspian Sea, U.S.S.R., (Bychowsky 1933a).

D. ALATUS Linstow, 1878.—*Blicca bjoerkna* (Linnaeus), Europe (Linstow 1878); Germany (Lühe 1909); Kostroma, U.S.S.R. (Bychowsky 1929, 1933); *Alburnus alburnus* (Linnaeus), Europe (Linstow 1878); Europe (Zandt 1924); U.S.S.R. (Bychowsky 1933); Sweden (Nybelin 1937).

D. AMPHIBOTHRIUM Wagener, 1857.—*Acerina cernua* (Linnaeus), Europe (Wagener 1857); Germany (Lühe 1909); East Prussia (Wegener 1909); Lake Beloje, U.S.S.R. (Bychowsky 1934); Karelian Lakes, U.S.S.R. (I. Bychowsky 1936); R. Kama, U.S.S.R. (Sachwatkin 1936); Sweden (Nybelin 1937). *Leuciscus leuciscus* (Linnaeus), R. Kama, U.S.S.R. (Sachwatkin 1936).

D. ANCHORATUS (Dujardin, 1845) Wagener, 1857.—*Cyprinus carpio* Linnaeus, Rennes, France (Dujardin 1845); (Diesing 1850); Vienna (Lühe 1909); East Prussia (Wegener 1909); U.S.S.R. (Bychowsky 1932); Ropscha, U.S.S.R. (Stoljarov 1934); Sweden (Nybelin 1937). *Carassius carassius* (Linnaeus), East Prussia (Wegener 1909); Poland (Kulwiec 1927); Kostroma, U.S.S.R. (Bychowsky 1929); Ropscha, U.S.S.R. (Stoljarov 1934); Sweden (Nybelin 1937). *Rutilus rutilus* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929). *Tinca tinca* (Linnaeus), Ropscha, U.S.S.R. (Stoljarov 1934).

D. APOGONIS Yamaguti, 1940.—*Apogon semilineatus* Temminck and Schlegel, Japan (Yamaguti 1940).

D. AURICULATUS (Nordmann, 1832) Diesing, 1850.—*Cyprinus carpio* Linnaeus, (Nordmann 1832); (Wedl 1857); Aral Sea, U.S.S.R., (Dogiel and Bychowsky 1933). *Abramis brama* (Linnaeus) (Nordmann 1832); Denmark (Krøyer 1852-3); (Wedl 1857); Belgium (van Beneden 1861); Sweden (Nybelin 1937). *Phoxinus phoxinus* (Linnaeus), Denmark (Krøyer 1852-3). *Carassius auratus* (Linnaeus), Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933). *Perca fluviatilis* (Linnaeus), Europe (Wagener 1857).

D. BICORNIS Malevitskaja, 1941.—*Rhodeus sericeus* (Pallas), U.S.S.R. (Malevitskaja 1941).

D. BINI Kikuchi, 1929.—*Anguilla japonica* (Temminck and Schlegel), Japan (Kikuchi 1929).

D. BOREALIS Nybelin, 1937.—*Phoxinus phoxinus* (Linnaeus), Sweden (Nybelin 1937).

D. CATLAIUS (Thapar, 1948).—*Catla catla*, India (Thapar 1948).

D. CHALCALBURNI Dogiel and Bychowsky, 1933.—*Chalcalburnus chalcoides* (Güldenstadt), Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933).

D. CHONDROSTOMI Malevitskaja, 1941—*Chondrostoma nasus* (Linnaeus), Dnjepr region, U.S.S.R. (Malevitskaja 1941).

D. CHRANILOWI Bychowsky, 1933.—*Abramis ballerus* (Linnaeus), Caspian Sea, U.S.S.R. (Bychowsky 1933a).

D. CORDUS Nybelin, 1937.—*Leuciscus leuciscus* (Linnaeus), Sweden (Nybelin 1937). *Leuciscus idus* (Linnaeus), Sweden (Nybelin 1937).

D. CORNU Linstow, 1878.—*Vimba vimba* (Linnaeus), Europe (Linstow 1878); Germany (Lühe 1909); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Blicca bjoerkna* (Linnaeus), East Prussia (Wegener 1909); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Sweden (Nybelin 1937). *Rutilus rutilus* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929). *Rutilus frisii* (Nordmann), U.S.S.R. (Bychowsky 1933). *Abramis brama* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929, 1933); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Leuciscus leuciscus* (Linnaeus), R. Kama, U.S.S.R. (Sachwatkin 1936).

D. CRASSUS Kulwiec, 1927.—*Cyprinus carpio* Linnaeus, Poland (Kulwiec 1927). *Carassius carassius* (Linnaeus), U.S.S.R. (Bychowsky 1932).

D. CRUCIFER Wagener, 1857.—*Scardinius erythrophthalmus* (Linnaeus), (Wagener 1857); Germany (Lühe 1909); East Prussia (Wegener 1909); U.S.S.R. (Bychowsky 1933). *Scardinius* sp., Lake Beloje, U.S.S.R. (Bychowsky 1934). *Rutilus rutilus* (Linnaeus), Germany (Lühe 1909); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933); Lake Beloje, U.S.S.R. (Bychowsky 1934); R. Kama, U.S.S.R. (Sachwatkin 1936); Karelian Lakes, U.S.S.R. (I. Bychowsky 1936); Sweden (Nybelin 1937). *Abramis brama* (Linnaeus), Europe (Zandt 1924); U.S.S.R. (Bychowsky 1933). *Blicca bjoerkna* (Linnaeus), Europe (Zandt, 1924); U.S.S.R. (Bychowsky 1933); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Alburnus alburnus* (Linnaeus), Europe (Zandt 1924); U.S.S.R. (Bychowsky 1933). *Leuciscus idus* (Linnaeus), R. Kama, U.S.S.R. (Sachwatkin 1936).

D. CRYPTOMERES Bychowsky, 1934.—*Cyprinus carpio* Linnaeus, Lake Beloje, U.S.S.R. (Bychowsky 1934). *Carassius carassius* (Linnaeus), Lake Beloje, U.S.S.R. (Bychowsky 1934). *Gobio gobio* (Linnaeus), Lake Beloje, U.S.S.R. (Bychowsky 1934); Dnjepr region, U.S.S.R. (Bychowsky 1933).

D. CYPRINI Buschkiel, 1930.—*Cyprinus carpio* Linnaeus, Java (Buschkiel 1930).

D. DIFFORMIS Wagener, 1857.—*Scardinius erythrophthalmus* (Linnaeus), Europe (Wagener 1857); Germany (Lühe 1909); Volga Delta, U.S.S.R. (Bychowsky 1933); Karelian Lakes, U.S.S.R. (I. Bychowsky 1936); Sweden (Nybelin 1937). *Squalius cephalus* (Linnaeus), East Prussia (Wegener 1909); Europe (Zandt 1924); Volga Delta, U.S.S.R. (Bychowsky 1933). *Cyprinus* sp., East Prussia (Wegener 1909). *Abramis brama* (Linnaeus), Volga Delta, U.S.S.R. (Bychowsky 1933). *Alburnus alburnus* (Linnaeus), Volga Delta, U.S.S.R. (Bychowsky 1933). *Blicca bjoerkna* (Linnaeus), Europe (Zandt 1924); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933).

D. DISTINGUENDUS Nybelin, 1937.—*Blicca bjoerkna* (Linnaeus), Sweden (Nybelin 1937.)

D. DRJAGINI Bychowsky, 1936.—*Diptychus dybowskii* Kessler, River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936).

D. DUJARDINIANUS (Diesing 1850) Diesing, 1858.—*Cyprinus carpio* Linnaeus, Europe (Diesing 1850). *Rutilus rutilus* (Linnaeus), (Diesing 1850); Europe (Linstow 1875). *Abramis brama* (Linnaeus), Belgium (van Beneden 1858, according to Diesing 1858).

D. FALCATUS (Wedl, 1857) Diesing, 1858.—*Cyprinus carpio* Linnaeus, Europe (Wedl 1857); cyprinoid fishes, Vienna (Lühe 1909). *Blicca bjoerkna* (Linnaeus), East Prussia (Wegener 1909). *Abramis brama* (Linnaeus), Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933); Sweden (Nybelin 1937).

D. FALLAX Wagener, 1857.—*Scardinius erythrophthalmus* (Linnaeus), (Wagener 1857); Europe (Taschenberg 1879); Germany (Lühe 1909); East Prussia (Wegener 1909); Europe (Zandt 1924); Sweden (Nybelin 1937). *Rutilus rutilus* (Linnaeus), (Wagener 1857); Europe (Taschenberg 1879); Germany (Lühe 1909); East Prussia (Wegener 1909); Europe (Zandt 1924); Kostroma, U.S.S.R. (Bychowsky 1929); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Sweden (Nybelin 1937). *Blicca bjoerkna* (Linnaeus), East Prussia (Wegener 1909); Kostroma, U.S.S.R. (Bychowsky 1929); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Leuciscus idus* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929). *Tinca tinca* (Linnaeus) Kostroma, U.S.S.R. (Bychowsky 1929). *Pelecus cultratus* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929). *Carassius carassius* (Linnaeus), Kostroma, U.S.S.R. (Bychowsky 1929). *Cyprinus carpio* Linnaeus, Kostroma, U.S.S.R. (Bychowsky 1929). *Leuciscus leuciscus* (Linnaeus), R. Kama, U.S.S.R. (Sachwatkin 1936).

D. FORMOSUS Kulwiec, 1927.—*Cyprinus* sp., Poland (Kulwiec 1927); Peterhof, (Bychowsky 1932). *Carassius carassius* (Linnaeus), U.S.S.R. (Bychowsky 1933); Sweden (Nybelin 1937).

D. FRATERNUS Wegener, 1909.—*Alburnus alburnus* (Linnaeus), East Prussia (Wegener 1909); U.S.S.R. (Bychowsky 1933); Sweden (Nybelin 1937). *Squalius cephalus* (Linnaeus), U.S.S.R. (Bychowsky 1933).

D. FRISII Bychowsky, 1933.—*Rutilus frisii kutum* (Kamensky), Caspian region, U.S.S.R. (Bychowsky 1933a).

D. GEMELLUS Nybelin, 1937.—Rutilus rutilus (Linnaeus), Sweden (Nybelin 1937).

D. GRACILIS Wedl, 1861.—*Hydrocynus dentex* (Forskal), Europe (Wedl 1861).

D. HAPLOGONUS Bychowsky, 1933.—*Vimba vimba persa* (Pallas), Caspian region, U.S.S.R. (Bychowsky 1933a).

D. KULWIECI Bychowsky, 1933.—*Barbus brachycephalus* Kessler, Caspian and Aral Seas, U.S.S.R. (Bychowsky 1931, 1933); Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933). *Barbus capito* (Güldenstadt), Caspian and Aral Seas, U.S.S.R. (Bychowsky 1931, 1933); Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933).

D. INTERMEDIUS Wegener, 1909.—*Carassius carassius* (Linnaeus), East Prussia (Wegener 1909); Poland (Kulwiec 1927); Peterhof, U.S.S.R. (Bychowsky 1932); Sweden (Nybelin 1937).

D. INVERSUS Goto and Kikuchi, 1917.—*Lateolabrax japonicus* (Cuvier and Valenciennes), Japan (Goto and Kikuchi 1917); Japan (Yamaguti 1938); Japan (Ishii and Sawada 1938). *Pneumatophorus japonicus* (Houttuyn), Japan (Ishii and Sawada 1938).

D. LINSTOWI Bychowsky, 1936.—*Schizothorax pseudaksaiensis* Herzenstein, River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936). *Barbus brachycephalus* Kessler, River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936).

D. LONGICOPULA Bychowsky, 1936.—*Schizothorax pseudaksaiensis* Herzenstein, River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936).

D. MACRACANTHUS Wegener, 1909.—*Tinca tinca* (Linnaeus), East Prussia (Wegener 1909); Germany (Wilde 1937); Sweden (Nybelin 1937).

D. MALLEUS Linstow, 1877.—*Barbus barbus* (Linnaeus), Europe (Linstow 1877); Europe (Sramek 1901); Germany (Lühe 1909). *Barbus brachycephalus* Kessler, Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933).

D. MEGASTOMA Wagener, 1857.—*Blicca bjoerkna* (Linnaeus), Europe (Wagener 1857). *Rhodeus amarus* (Bloch), Europe (Wagener 1857); Germany (Lühe 1909). *Esox lucius* Linnaeus, Europe (Wagener 1857).

D. MERIDIONALIS Bychowsky, 1936.—*Nemacheilus stoliczkai* (Steindachner), River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936). *Nemacheilus dorsalis* (Kessler), River Tschu, Kirghiz, U.S.S.R. (Bychowsky 1936).

D. MICRACANTHUS Nybelin, 1937.—*Rutilus rutilus* (Linnaeus), Sweden (Nybelin 1937).

D. MINOR Wagener, 1857.—*Alburnus alburnus* (Linnaeus), Europe (Wagener 1857); Germany (Lühe 1909); East Prussia (Wegener 1909); Europe (Zandt 1924); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Sweden (Nybelin 1937). *Blicca bjoerkna* (Linnaeus), Germany (Lühe 1909); Europe (Zandt 1924).

D. MINUTUS Kulwiec, 1927.—*Cyprinus carpio* Linnaeus, Poland (Kulwiec 1927); Sweden (Nybelin 1937).

D. MOLLIS Wedl, 1857.—*Cyprinus carpio* Linnaeus, Europe (Wedl 1857); Vienna (Lühe 1909). *Tinca tinca* (Linnaeus), U.S.S.R. (Bychowsky 1929). *Alburnus alburnus* (Linnaeus), U.S.S.R. (Bychowsky 1929).

D. MOORTHYI Price, 1938.—*Puntius puckelli* Day and *Puntius ticto* (Hammer and Buchwald), Chitaldrug, Mysore State, India (Price 1938).

D. NANUS Dogiel and Bychowsky, 1933.—*Rutilus rutilus* (Linnaeus), Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933); R. Kama, U.S.S.R. (Sachwatkin 1936). *Abramis brama* (Linnaeus), Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933).

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D. PROPINQUUS Bychowsky, 1931.—*Abramis sapa* (Pallas), Aral Sea, U.S.S.R. (Bychowsky 1931).

D. PUNTII Buschkiel, 1930.—*Puntius lateristriga* (Cuvier and Valenciennes), Java (Buschkiel 1930).

D. RAMULOSUS Malevitskaja, 1941.—*Leuciscus idus* (Linnaeus), Kiew, U.S.S.R. (Malevitskaja 1941).

D. ROBUSTUS Malevitskaja, 1941.—*Leuciscus idus* (Linnaeus) and *Aspius aspius* (Bleeker), Dnjepr River, U.S.S.R. (Malevitskaja 1941).

D. SIMILIS Wegener, 1909.—*Rutilus rutilus* (Linnaeus), East Prussia (Wegener 1909); Europe (Zandt 1924); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Sweden (Nybelin 1937).

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D. SIMPLICIMALLEATUS (Bychowsky, 1931) Sproston, 1946.—*Pelecus cultratus* (Linnaeus), Aral Sea, U.S.S.R. (Bychowsky 1931); Lake Beloje, U.S.S.R. (Bychowsky 1934).

D. SPHYRNA Linstow, 1878—*Vimba vimba* (Linnaeus), (Linstow 1878); East Prussia (Wegener 1909). *Abramis brama* (Linnaeus), Germany (Lühe 1909); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Blicca bjoerkna* (Linnaeus), East Prussia (Wegener 1909); Kostroma, U.S.S.R. (Bychowsky 1929); Lake Beloje, U.S.S.R. (Bychowsky 1934); U.S.S.R. (Bychowsky 1933); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Rutilus rutilus* (Linnaeus), Europe (Zandt 1924); Kostroma, U.S.S.R. (Bychowsky 1929); U.S.S.R. (Bychowsky 1933); Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Karelian Lakes, U.S.S.R. (I. Bychowsky 1936); R. Kama, U.S.S.R. (Sachwatkin 1936).

D. SUECICUS Nybelin, 1937.—*Rutilus rutilus* (Linnaeus), Sweden (Nybelin 1937).

D. TENUIS Wedl, 1857.—*Perca fluviatilis* (Linnaeus), Europe (Wedl 1857); Vienna (Lühe 1909).

D. TUBA Linstow, 1878.—*Squalius cephalus* (Linnaeus), Europe (Linstow 1878);

Germany (Lühe 1909). *Leuciscus leuciscus* (Linnaeus), Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933). *Leuciscus idus* (Linnaeus), R. Kama U.S.S.R. (Sachwatkin 1936); Sweden (Nybelin 1937). *Aspius aspius* (Bleeker, Aral Sea, U.S.S.R. (Dogiel and Bychowsky 1933); Sweden (Nybelin 1937).

D. UNCINATUS Wagener, 1857.—*Perca fluviatilis* (Linnaeus), Europe (Wagener 1857).

D. VASTATOR Nybelin, 1924.—*Cyprinus carpio* Linnaeus, Sweden (Nybelin 1924); Poland (Kulwiec 1929); U.S.S.R. (Bychowsky 1932); Ropscha, U.S.S.R. (Stoljarov 1934). *Carassius carassius* (Linnaeus), U.S.S.R. (Bychowsky 1932); Ropscha, U.S.S.R. (Stoljarov 1934); Kyoto, Japan (Yamaguti 1940). *Cyprinus* sp., Kyoto Japan (Yamaguti 1940).

D. WEGENERI Kulwiec, 1927.—*Cyprinus* sp., Poland (Kulwiec 1927); U.S.S.R. (Bychowsky 1932). *Carassius carassius* (Linnaeus), Sweden (Nybelin 1937).

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D. ZANDTI Bychowsky, 1933.—*Blicca bjoerkna* (Linnaeus), Leningrad and Caspian Sea, U.S.S.R. (Bychowsky 1933a); Lake Constance (Zandt 1924); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933). *Abramis brama* (Linnaeus), Leningrad and Caspian Sea, U.S.S.R. (Bychowsky 1933a); Newabucht, U.S.S.R. (Dogiel and Petruschewsky 1933); Sweden (Nybelin 1937).

NOMINA NUDA: *D. aequans* Wagener, 1857. *D. echeneis* Wagener, 1857.. *D. elongatus* Jacob, 1940. *D. major* Wagener, 1857. *D. paradoxus* (Creplin, 1839). *D. pedatus* Wagener, 1857. *D. siluri* Wagener, 1857. *D. trigonodistoma* Wagener, 1857.

Appendix III

WORLD LIST OF DACTYLOGYRUS HOSTS

ANGUILLIDAE

ANGUILLA JAPONICA (Temminck and Schlegel)—*Dactylogyrus bini.*

CATOSTOMIDAE

HYPENTELIUM NIGRICANS (LeSueur)—*D. apos.* MOXOSTOMA ANISURUM (Rafinesque)—*D. urus.* MOXOSTOMA DUQUESNI (LeSueur)—*D. duquesni.*

CHARACIDAE

HYDROCYNUS DENTEX (Forskal)—*D. gracilis.*

CHEILODIPTERIDAE

Apogon semilineatus Temminck and Schlegel—*D. apogonis.*

COBITIDAE

NEMACHEILUS DORSALIS (Kessler)—*D. meridionalis.* NEMACHEILUS STOLICZKAI (Steindachner)—*D. meridionalis.*

CYPRINIDAE

ABRAMIS BALLERUS (Linnaeus)—*D. chranilowi.* ABRAMIS BRAMA (Linnaeus)—*D. auriculatus, D. cornu, D. crucifer, D. difformis, D. dujardinianus, D. falcatus, D. nanus, D. sphyrna, D. wunderi, D. zandti.* ABRAMIS SAPA (Pallas)—*D. propinquus.* ACROCHEILUS ALUTACEUS Agassiz and Pickering—*D. vancleavei.* ALBURNUS ALBURNUS (Linnaeus)—*D. alatus, D. crucifer, D. difformis, D. fraternus, D. minor, D. mollis, D. parvus.* ASPIUS ASPIUS (Bleeker)—*D. robustus, D. tuba.* BARBUS BARBUS (Linnaeus)—*D. malleus.* BARBUS BRACHYCEPHALUS Kessler—*D. affinis, D. kulwieci, D. linstowi, D. malleus.* BARBUS CAPITO (Güldenstadt)—*D. kulwieci.* BLICCA BJOERKNA (Linnaeus)—*D. alatus, D. cornu, D. crucifer, D. difformis, D. distinguendus, D. falcatus, D. fallax, D. megastoma, D. minor, D. sphyrna, D. wunderi, D. zandti.*

CAMPOSTOMA ANOMALUM (Rafinesque)—*D. acus, D. Campostomus,* CARASSIUS AURATUS (Linnaeus)—*D. anchoratus, D. auriculatus.* CARASSIUS CARASSIUS (Linnaeus) *D. anchoratus, D. crassus, D. cryptomeres, D. fallax, D. formosus, D. intermedius, D. vastator, D. wegeneri.* CHALCALBURNUS CHALCOIDES—(Güldenstadt)—*D. chalcalburni.* CHONDROSTOMA NASUS (Linnaeus)—*D. chondrostomi.* CLINOSTOMUS ELONGATUS (Kirtland)—*D. confusus.* COUESIUS PLUMBEUS DISSIMILIS (Girard)—*D. banghami, D. mylocheilus.* CYPRINUS CARPIO Linnaeus—*D. anchoratus, D. auriculatus D. crassus, D. cryptomeres, D. cyprini, D. dujardinianus, D. extensus, D. falcatus, D. fallax, D. minutus, D. mollis, D. vastator.* CYPRINUS sp.—*D. difformis, D. formosus, D. vastator. D. wegeneri.* DIPTYCHUS DYBOWSKII Kessler—*D. drjagini, D. simplex.* ERYCIMBA BUCCATA Cope—*D. cornutus, D. superficialis.* EXOGLOSSUM MAXILLINGUA (LeSueur)—*D. scutatus.* GOBIO GOBIO (Linnaeus)—D. cryptomeres.

HYBOGNATHUS P. PLACITA Girard.—*D. banghami, D. hybognathus.* HYBOPSIS AMBLOPS (Rafinesque)—*D. amblops.* HYBORHYNCHUS NOTATUS (Rafinesque)—*D. bifurcatus, D. bychowskyi, D. simplexus.* HYDROCYNUS DENTEX (Førskal)—*D. gracilis.* LEUCISCUS IDUS (Linnaeus)—*D. cordus, D. crucifer, D. elongatus, (nomen nudum), D. fallax, D. ramulosus, D. robustus, D. tuba.* LEUCISCUS LEUCISCUS (Linnaeus)—*D. amphibothrium, D. cordus, D. cornu, D. fallax, D. tuba.* MYLOCHEILUS CAURINUS (Richardson)—*D. mylocheilus.* NOTEMIGONUS CRYSOLEUCAS AURATUS (Rafinesque)—*D. aureus, D. parvicirrus.* NOTEMIGONUS C. CRYSOLEUCAS (Mitchill)—*D. aureus, D. parvicirrus.* NOTROPIS CORNUTUS (Agassiz)—*D. acus, D. banghami, D. bulbus, D. bullosus, D. cornutus, D. fulcrum, D. perlus, D. pollex.* NOTROPIS CORNUTUS FRONTALIS (Agassiz)—*D. dubius, D. pyriformis, D. vannus.* NOTROPIS DELICIOSUS MISSURIENSIS (Cope)—*D. banghami, D. moorei.* NOTROPIS GIRARDI (Hubbs and Ortenburger) —*D. banghami.* NOTROPIS L. LUTRENSIS (Baird and Girard)—*D. banghami, D. moorei.* NOTROPIS PERCOBROMUS (Cope)—*D. banghami, D. percobromus.* NOTROPIS PHOTOGENIS (Cope)—*D. photogenis.* NOTROPIS RUBELLUS (Agassiz)—*D. orchis, D. rubellus.* NOTROPIS UMBRATILIS ATRIPES (Jordan)—*D. confusus, D. umbratilis.* NOTROPIS VOLUCELLUS BUCHANANI Meek.—*D. banghami.* NOTROPIS V. VOLUCELLUS (Cope) —*D. distinctus.* NOTROPIS WHIPPLII (Agassiz and Pickering) — *D. confusus, D. whipplius.*

PAREXOGLOSSUM LAURAE Hubbs—*D. scutatus.* PELECUS CULTRATUS (Linnaeus)— *D. fallax, D. simplicimalleatus.* PHENACOBIUS MIRABILIS (Girard)—*D. phenacobius.* PHOXINUS PHOXINUS (Linnaeus)—*D. auriculatus, D. borealis.* PTYCHOCHEILUS OREGONENSIS (Richardson)—*D. columbiensis, D. vancleavei, D. ptychocheilus, D. tridactylus.* PUNTIUS LATERISTRIGA (Cuvier and Valenciennes)—*D. puntii.* PUNTIUS PUKELLI Day —*D. moorthyi.* PUNTIUS TICTO (Hammer and Buchwald)—*D. moorthyi.* RHINICHTHYS CATARACTAE (Valenciennes)—*D. banghami.* RHODEUS AMARUS (Bloch)—*D. megastoma.* RHODEUS SERICEUS (Pallas)—*D. bicornis.* RICHARDSONIUS BALTEATUS (Richardson)—*D. banghami, D. richardsonius.* RUTILUS FRISII (Nordmann)—*D. cornu, D. nybelini.* RUTILUS FRISII KUTUM (Kamensky)—*D. frisii.* RUTILUS RUTILUS (Linnaeus)—*D. anchoratus, D. cornu, D. crucifer, D. dujardinianus, D. fallax, D. gemellus, D. micracanthus, D. nanus, D. similis, D. sphyrna, D. suecicus.*

SCARDINIUS ERYTHROPHTHALMUS (Linnaeus)—*D. crucifer, D. difformis, D. fallax.* SCARDINIUS sp.—*D. crucifer.* SCHIZOTHORAX PSEUDAKSAIENSIS Herzenstein—*D. linstowi, D. longicopula.* SEMOTILUS ATROMACULATUS (Mitchill)—*D. atromaculatus, D. microphallus, D. semotilus, D. tenax.* SEMOTILUS A. ATROMACULATUS (Mitchill)—D. *attenuatus, D. claviformis, D. lineatus.* SQUALIUS CEPHALUS (Linnaeus)—*D. difformis, D. fraternus, D. parvus, D. tuba.* TINCA TINCA (Linnaeus)—*D. anchoratus, D. fallax, D. macracanthus, D. mollis.* VIMBA VIMBA (Linnaeus)—*D. cornu, D. sphyrna.* VIMBA VIMBA PERSA (Pallas)—*D. haplogonus.*

ESOCIDAE

ESOX LUCIUS Linnaeus—*D. megastoma.*

GASTEROSTEIDAE

EUCALIA INCONSTANS (Kirtland)—*D. eucalius.*

PERCIDAE

ACERINA CERNUA (Linnaeus)—*D. amphibothrium.* PERCA FLUVIATILIS (Linnaeus) —*D. auriculatus, D. tenuis, D. uncinatus.*

SCOMBRIDAE

PNEUMATOPHORUS JAPONICUS (Houttuyn)—*D. inversus.*

SERRANIDAE

LATEOLABRAX JAPONICUS (Cuvier and Valenciennes)—*D. inversus.*

SUMMARY

Dactylogyrus banghami Mizelle and Donahue, 1944, is comparatively described and nine new species of *Dactylogyrus* are described from British Columbia, Ontario (Canada), and Oklahoma as follows: *D. columbiensis, D. ptychocheilus,* and *D. tridactylus* all from *Ptychocheilus oregonensis; D. vancleavei* from *Ptychocheilus oregonensis* and *Acrocheilus alutaceus; D. mylocheilus* from *Mylocheilus caurinus* and *Couesius plumbeus dissimilis; D. richardsonius* from *Richardsonius balteatus* all from British Columbia; *D. hybognathus* from *Hybognathus p. placita; D. moorei* from *Notropis l. lutrensis* and *Notropis deliciosus missuriensis; D. percobromus* from *Notropis percobromus* all from Oklahoma; *D. banghami* was recovered from all three areas. New distribution records for *D. anchoratus* (Dujardin, 1845) and *D. extensus* Mueller and Van Cleave, 1932, are reported from British Columbia.

The genus *Neodactylogyrus* Price, 1938 is rejected on the basis of an unreliable, highly variable, and vestigial ventral bar. The genus *Paradactylogyrus* Thapar, 1948, demands more study before acceptance since the occurrence of a single haptoral spicule is not thought to be of generic magnitude.

A table showing the number of valid species of *Dactylogyrus* with the number of different hosts infested by each indicates that 61.95% infest one host each, 24.78% infest a total of two different host species, 5.31% infest three host species, and 7.94% infest four or more host species. These data show that host specificity in this group may not be as narrow as previously recognized (Bychowsky 1933).

North American and Old World species of *Dactylogyrus* are listed according to hosts and other pertinent data (Appendices I, II).

A world host-infestation list is presented which includes only the accepted host names and the *Dactylogyrus* species found thereon (Appendix III).

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Phylogeny and Taxonomy of the Compositae

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The Compositae have long attracted attention as a well marked but highly variable group, so distinct as to render their affinities doubtful. A number of efforts to elucidate their phylogeny have been made in the near-century since Darwin, without conspicuous success. This paper represents an effort to summarize the information available on the origin of the family, and on the evolutionary developments and broad relationships within the group. On many points the evidence permits a reasoonably firm conclusion; other items remain doubtful, and await further studies not only of the Compositae but of their possible ancestors.

The recognition of the Compositae as a distinct group dates back at least several hundred years, and probably even to Theophrastus (see historical summary by Small, 1917). Linnaeus was so impressed with the unity of the group that he departed from the general principles of his sexual system to unite the genera into his class Syngenesia. Although some of the tribes, notably the Cichorieae and Cynareae, were evidently recognized by pre-Linnaean authors, the establishment and delimitation of the tribes was essentially the work of Cassini (1826, 1829, 1834). Some of his tribes are now received as sub-tribes, but the basic outlines of his organization remain.

The most monumental contribution to our understanding of the family is that of George Bentham, as shown in the *Genera Plantarum* and in his separate paper (1873) on the family. After 80 years, his system stands essentially unaltered, and his tentative speculations on phylogeny are in my opinion more nearly correct than those of any of his successors. It may not be generally realized, however, that his treatment of the Compositae and other groups in the *Genera Plantarum,* while it attempted to be natural, was not phylogenetic in the modern sense of the term. He attempted to put related things together, and to arrive at a concept of relationships by considering the whole ensemble of characters rather than by assigning fixed arbitrary values to individual characters, but he did not necessarily start with the most primitive group and proceed to the most specialized. Thus, although he suggests (1873, p. 482) that the Heliantheae come the nearest of all the tribes to matching the necessary characters of the hypothetical progenitor of the group, the sequence of tribes in the *Genera Plantarum* starts with the Vernonieae, and places the Heliantheae near the middle, as the fifth tribe.

I quote:

"Some confirmation of the hypothesis that some of the oldest of the primary tribual and subtribual types of the Compositae are to be sought for in the Helianthoideae . . . may perhaps be derived from their structure. The great consolidation and uniform structure of the essential organs of fructification of the Compositae has, as already mentioned, been adduced as evidence of their comparatively recent origin; and this consolidation and uniformity is least marked in the Helianthoideae. . . . In many Helianthoideae we find, for instance, the outer bracts of the involucre more foliaceous, the bracts subtending the

flowers (or receptacular paleae) more normally and more firmly attached, the calyx-limb (or pappus) less transformed, consisting frequently of persistent teeth or aristae directly continuous with the ribs of the ovary, and thus showing their really calycine nature."

In a pregnant if somewhat obscure paragraph a little further on (pp. 483-4), Bentham recognizes the close consanguinuity of the Eupatorieae, Vernonieae, Cynareae, and Mutisieae, and seems to consider this group of tribes similar, in age and degree of modification from the original type, to the Heliantheae. He relates the Cichorieae also to the hypothetical prototype, but considers them to be of relatively more recent origin.

In my opinion, these suggestions, published only 14 years after Darwin's Origin of Species, in a paper not primarily concerned with phylogeny, come much closer to the truth than any of the phylogenetic schemes subsequently proposed. I would question chiefly his natural assumption that the primitive Composite was discoid, and that the Eupatorieae, Vernonieae, and Cynareae are primitively rather than secondarily discoid. More of this anon. He notes the essentially parallel nature of the Eupatorieae, Vernonieae, Cynareae, and Mutisieae, deriving these from a more primitive common ancestor rather than relating them ancestrally to one another. He indicates the independent origin of the cichoriaceous type of ray from the ray of the radiate tribes. Although he fails to indicate at this point the close connection between the Mutisieae and Cichorieae, that connection is noted elsewhere in the paper. The Cichorieae, although certainly allied to the Mutisieae, do not appear to be derived from the latter, but again from a common ancestor instead. This is precisely the relationship indicated by Bentham's paper.

Hoffman's treatment of the Compositae for *Die natürlichen Pflanzenfamilien* was similar to that of Bentham, differing only in details. He used the same sequence of tribes, which dates from DeCandolle. Whereas Bentham accepted that sequence more from the standpoint of tradition and convenience than from conviction, the principles of the Englerian system (which equated the simple with the primitive) forbade starting with the Heliantheae or any other radiate tribe. With the general dominance of the Englerian system, the Vernonieae have often been assumed to be the most primitive tribe of the family. A recent, scholarly discussion by Augier and Du Merac (1951) concludes that the Vernonieae are primitive and were so designated by Bentham (which they were not).

Various rebels have from time to time proposed other suggestions. Small (1917 et seq.) considered the Senecioneae to be the basic group. His conclusion was founded in large part on the Willisian concept of direct correlation between age of a group and number of its species. Since *Senecio* is by far the largest genus in the family, it was necessarily considered the oldest, and Small did his best to derive the rest of the family from it. Modern taxonomists see no such precise correlation between age, area, and number of species as did Willis. Being without foundation, Small's scheme cannot stand. Its incompatability with the evidence is ably elucidated by Augier and Du Merac. Recognizing some of the primitive features of the Heliantheae, Small repeatedly found it necessary to refer to the "atavistic" tendencies of this tribe. More explicitly, he says in one place that the "tendency to revert to a pre-Composite ancestor . . . attains its highest development in this tribe" (1918, p. 131).

Bessey (1915) and Hutchinson (1916) considered the Heliantheae to be the most primitive tribe of the Compositae. Humbert (1927) has by implication suggested the Heliantheae as primitive within the family, although the plant which provoked his observations proves to be a species of *Sphaeranthus* (Inuleae) with reduced, 3-flowered heads aggregated into a bracteolate secondary head. Wodehouse (1928a) considered the pollen of the Heliantheae to represent the most primitive or characteristic type in the family, from which other types might be derived. A genus of the Heliantheae (*Hoffmanniella*) was suggested by Lawalree (1943) as being very primitive within the family. The quotation from Stebbins reproduced elsewhere in this paper indicates that he considers the Heliantheae as the most primitive tribe, and the late Dr. F. W. Pennell suggested to me in conversation in 1940 that the Heliantheae were the basal group of the family. I am under the impression that there has been a widespread private acceptance of this point of view by American taxonomists, at least, in spite of the lack of any definitive exposition of the thesis.

Recently Leonhardt (1949) has suggested that the Cynareae are the most primitive tribe of the family. I see nothing to support this view. The spiny habit, hardly foliaceous involucres, mostly bristly rather than chaffy receptacles, caudate anthers, and modified styles that characterize this tribe surely preclude any possibility of its being ancestral to the others.

A study of either the ancestry or the lines of development within the Compositae necessarily involves a consideration of what are the primitive characters in the group. Whatever hypotheses are held as to the relationships of the Compositae it seems obvious that they are derived from sympetalous, epigynous ancestors, that the head is a condensed inflorescence, and that both the involucral and receptacular bracts are modified leaves. Bearing these and other facts in mind, the following features are here suggested as being primitive within the group.

1. Habit herbaceous
2. Leaves opposite
3. Heads few, each with many flowers
4. Involucre leafy, several-seriate
5. Receptacle chaffy
6. Rays present, pistillate, fertile
7. Disk-flowers perfect, fertile
8. Lobes of the disk-corollas with well developed midvein
9. Corollas yellow, the pigments partly or wholly carotinoid
10. Pappus chaffy, of 5 members
11. Anthers connate, not tailed
12. Stigmatic portion of the style branches not clearly differentiated, or the branches largely stigmatic within.

The reasons for each of these suggestions will be discussed in turn.

Habit.—The vast majority of the Compositae are herbaceous, and the woody groups are not closely related among themselves. Each woody group, on the contrary, has generally its herbaceous counterpart, *Olearia* with *Aster*, the woody Senecios with the other Senecios, the woody Haplopappi with the other Haplopappi, the woody Artemisiae with the other Artemisiae, etc. Furthermore, the woody types that have been studied do not resemble each other anatomically, but tend toward the development of diverse types of anomalies. The most striking of these anomalies is presented by several woody genera of the Inuleae, which have no primary cambium, and in which the secondary thickening is due to an adventitious or secondary cambium developing from the parenchyma tissues of the pericycle (Adamson, 1934). Some other woody types, such as the arborescent African Senecios, retain

the large pith and some other features more characteristic of herbs (Hare, 1941; Cotton, 1944). It thus seems clear that many of the woody Compositae have been derived from herbaceous ancestors within the family. While it is not yet certain that this is true in all cases, the burden of proof rests with anyone who suggests that any particular woody Composite is primitively woody.

Many of the herbaceous genera of the family, however (e.g., *Helianthus*) do have an active cambium. When such genera grow in warm regions, so that the stem is not killed back to the ground each year, they might be expected to become shrubby without any great genetic change. It should therefore not be surprising that woody Compositae are more common in tropical and subtropical regions than in the temperate zone, although of course they are not wholly so restricted. Some of these woody groups, as already noted, show clearly by their anatomy that they are derived from herbs, and others, such as the large, regularly frutescent, and chiefly tropical genus *Baccharis* are evidently specialized in other features and can be related to the rest of the family only through herbaceous genera. It is of course not impossible that a secondarily woody group may again give rise to herbaceous members, so that within a given genus the woody species are the more primitive. Since all of the tribes are predominantly herbaceous, and most of them contain some woody members, no evidence as to the relative advancement of the tribes can be drawn from this feature.

Leaf arrangement.—The greater number of genera of the Compositae have alternate leaves, but many (chiefly among the Heliantheae and Eupatorieae) have opposite leaves, and a few (chiefly among the Eupatorieae) have whorled leaves. One of the principal reasons for considering the opposite arrangement of leaves to be primitive within the family is that it is only by starting with th predominantly opposite-leaved Heliantheae that one can make a satisfactory arrangement of the tribes. Nearly all of the other radiate tribes connect to and appear to be derived from the Heliantheae. The sole exception is the Calenduleae, a small group which is obviously derived from the Senecioneae and which might indeed be included in that tribe without loss of naturalness. The discoid tribes tend to stand apart as a group distinct from the radiate tribes, but all of the discoid tribes are excluded on other morphological grounds from serious consideration as being primitive within the family. As elsewhere noted, there are, furthermore, connections between the discoid and radiate tribes.

Although the Heliantheae show a strong tendency toward opposite leaves, a few genera have the leaves wholly alternate, and a great many of the species tend to have some of the upper leaves, or even all but the lowermost leaves alternate. The principle of recapitulation would suggest that the opposite-leaved condition is primitive, and that those Heliantheae with the upper leaves alternate represent a stage intermediate between regularly opposite and regularly alternate leaves. Although uncritical application of the principle of recapitulation could lead to some bizarre conclusions in other groups, it seems worth noting that here the evidence from ontogeny is concordant with evidence from other sources. As has been pointed out by Stebbins (1950) and others, whatever validity is possessed by the principle of recapitulation is due to the fact that the expression of a gene may appear at any stage of ontogeny, so that in many cases contin-

ued evolutionary development leaves the earlier ontogenetic stages unchanged.

The spiral, centripetal (indeterminate) arrangement of the flowers in a Composite head (corresponding to an alternate-leaved phyllotaxy) has been adduced by Leonhardt (1949) as an argument against relating the Compositae to the predominantly opposite-leaved, dichasial Rubiales. He properly points out that condensation of a rubialean type of inflorescence leads to the type of head found in the Dipsacaceae, with anatomical and morphological evidences of the ancestral condition. Since the capitula of the Compositae are merely the termini of their respective branches, however, and since we have already noted a shift from opposite to alternate leaves, progressing from the top downwards, this argument loses its validity. It would seem more reasonable to consider the alternate (spiral) phyllotaxy of the heads as merely the first step in the change from an opposite-leaved dichasial ancestry to the presently more prevalent, wholly alternate-leaved condition. The derivation of a centripetal sequence of flowering from a centrifugal one is not impossible nor even always very difficult (Rickett, 1944); the change is apparently underway in species of *Cephalaria* (Dipsacaceae) which have a mixed sequence, with the outermost row of flowers blooming first. The fact that the sequence of flowering *among* the heads of the Compositae is almost wholly centrifugal (determinate) bespeaks a dichasial ancestry for the group. The curious reversal between the sequence of flowering within a head and the sequence among the heads becomes more understandable in the light of the foregoing suggestions.

Number of heads and flowers, and nature of the involucre.—Since the head in the Compositae represents in reality an inflorescence, it seems reasonable to expect the hypothetical prototype to have few or solitary, numerously flowered heads. Likewise, since the involucral bracts are essentially leaves, the foliaceous type of involucral bract should be considered primitive. Various genera or individual species may have some of the uppermost leaves crowded around the involucre, and removed from the more normally developed leaves, but still sharply differentiated from the involucre proper. This repetition of the process which led to the formation of the involucre is of course an evolutionary advance, even though at first glance the involucre appears to be leafy.

Nature of the receptacle.—The receptacular bracts ordinarily subtend the individual flowers of the head, and are clearly homologous with the bracts subtending the individual flowers in an ordinary raceme. The chaffy receptacle (bracts present) would therefore be more primitive than the naked receptacle (bracts absent). It might be expected that the primitive receptacle would be more or less elongate, and the fact that elongate receptacles are found chiefly in scattered genera of the Heliantheae lends some credence to the suggestion. The Heliantheae with elongate receptacles do not appear on other grounds to be especially primitive within the tribe, however, and the elongation of the receptacle in several genera of the Inuleae is almost certainly secondary. I would therefore reserve judgement as to the primitive shape of the Composite receptacle.

Nature of the flowers.—It has been the traditional concept that the discoid Composite head is primitive, and the radiate head derived. This follows the general evolutionary principle that the specialized is derived from

the generalized, and it seems at first glance to have the virtue of simplicity. If this concept is to be accepted, however, it must be restricted in its application to the discoid tribes. Throughout the radiate tribes there is a repeated tendency toward reduction of the rays, as has been noted by numerous authors. Discoid individuals, species, genera, and sub-tribes are clearly related to and derived from radiate taxa. This repeated loss of the rays warrants the assumption that for the radiate tribes as a group the radiate condition is primitive, and any discoid member has a radiate ancestry.

As regards the discoid tribes, the evidence is conflicting. It would certainly seem possible to derive the discoid Cynareae from something like the radiate Arctotideae, and discoid members of the Arctotideae are in fact sometimes distinguished from the Cynareae only with considerable difficulty. If the Cynareae are discoid by reduction, then the same interpretation could readily (and almost necessarily) be extended to include the Vernonieae and Eupatorieae. In the Mutisieae, on the other hand, the situation is quite different. Instead of finding evidences of reduction and loss of ligules, we find every transition between the simple, tubular disk-corolla and the characteristic rays of the radiate tribes, and also every transition from the tubular corolla to the characteristic ray of the Cichorieae. The Mutisieae being closely allied to the Cichorieae, we have here good evidence that the ligulate heads charactristic of the Cichorieae have been derived within the family from the discoid head. One should point out, however, that the development of an essentially ligulate head in a few Mutisieae represents a case of close parallelism, for on other morphological grounds it is difficult to derive the Cichorieae from any except perhaps the very basal part of the Mutisieae. It has been generally accepted among synantherologists that the lamina of the ray in tribes other than the Chicorieae is composed of 3 lobes of the corolla, with the inner 2 (the upper) lobes suppressed, and Small (1918) has pointed out numerous normal and teratological examples among the radiate tribes in which the vestiges of these 2 upper lobes are more or less evident. Since the Mutisieae are not closely allied to any of the radiate tribes, however, it does not seem possible for the latter to have inherited their rays from the Mutisieae. Here again we have a case of parallelism. The question is whether the discoid tribes and the discoid Mutisieae are primitively discoid, in which case the 3-toothed ray of the radiate tribes has been developed within the family in a fashion similar to its development in the Mutisieae; or whether the discoid tribes are secondarily discoid, in which case the differentiation of the marginal flowers occurred during or before the differentiation of the family, and the similar rays of some of the Mutisieae are independently developed after having once been lost. The evidence presently available does not permit a firm conclusion. From the clearly secondary nature of discoidy among the radiate tribes, from the close relation of the Cynareae to the Arctotideae, and from the fact that the discoid tribes do not appear to be primitive in other respects, I am inclined to the belief that the primitive Composite was radiate, and that all discoidy within the family as it now exists is derived. A litle reflection will show that such a position is not unreasonable. The very Composite-like heads of *Cephalaria* (Dipsacaceae), with expanded, irregular marginal flowers, show a similar differentia-

tion in form and function of the flowers, although the rays are not structurally identical to those of the Compositae. The familiar *Viburnum*, a member of the Rubiales, often has the outer flowers of the inflorescence enlarged and sterile, and similar tendencies can be seen as far down the evolutionary scale as *Heracleum*, in the Umbelliferae, and *Hydrangea*, in the Saxifragaceae. There is thus no inherent reason why the differentiation of the marginal flowers may not have accompanied or even preceded the evolution of the Compositae from their less specialized sympetalous ancestors.

Among the radiate tribes, the rays vary from pistillate and fertile, to pistillate (i.e., with a style) and sterile, to neutral (without a style). Within the general framework of modern evolutionary thought regarding the angiosperms, it seems unnecessary to defend the choice of the pistillate and fertile condition of the rays as being more primitive than the neutral condition, with the pistillate but sterile condition representing an intermediate step. Likewise, the perfect condition of the disk-flowers is evidently more primitive than the functionally staminate condition.

Dr. Minna Koch (1930) has studied the vascular anatomy of the ray and disk-flowers of a number of species of Compositae in various tribes. She concludes that the familiar pattern of vascularization of the disk-flowers (in which the veins are directed toward the sinuses, there to fork, with adjacent forks anastomosing at the tips of the lobes) is a result of reduction from the venation of a primitive sympetalous corolla by fusion of the lateral bundles of adjacent corolla-lobes, and suppression of the central bundle of each lobe. A similar interpretation had been casually suggested by Bentham more than half a century earlier (1873, p. 366). Dr. Koch states that the Heliantheae differ from the rest of the family in the retention of the central bundle, but this is in reality a mere tendency, better expressed in some genera than in others, and quite wanting in many, rather than a definitive tribal character. This tendency toward a relatively primitive vascularization of the disk-flowers of the Heliantheae (stated in more positive form by Dr. Koch) supports the basal position assigned to that tribe in this paper.

Dr. Koch's interpretation of the anatomy and morphology of the ray-flowers is more controversial. She states that the Heliantheae are sharply distinguished from the other tribes by the presence of two or three strong bundles which stand out on the lower surface of the ray. Chiefly because these are not medially embedded in the ray, she considers that "It is clear that these extra veins are not a part of the true corolla, but something accessory." She lightly dismisses the relation between the veins and the apical lobes of the ray, by citing the absence of relation between the venation and lobing in genera elsewhere in the family with more reduced rays. By a further tortuous argument she concludes that these larger bundles are really calycine, and thus presumably that the heliantheous ray is a combination of calyx and corolla. Since she considers (as I do) that the smaller rays with less complex vascularization found elsewhere in the family are reduced types, with various stages of reduction both in vascularization and external morphology still preserved, it is to be presumed that she considers the rays of the other tribes also to represent combinations of calyx and corolla.

It is true that a large proportion (though not all) of the Heliantheae have two large veins which stand out on the lower surface of the ray. These tend to be directed to the apical sinuses, there often to fork after the manner of the veins of the disk-corollas. The same pattern can be observed, however, in various genera in other tribes, especially those which have larger and firmer rays. Oftentimes, especially in the Heliantheae, there is a third, somewhat less prominent large vein which is medial in position and thus directed to the central tooth. And in some of the Heliantheae, notably in *Blepharipappus* and some species of *Madia*, the three large veins are directed to the three well marked lobes of the ray. With the reduction of the rays that occurs widely throughout the family, the two large veins gradually cease to be more prominent than the others, and may even disappear, so that there is then no relation between the lobing and the venation.

I see no good reason to assume that these two or three larger bundles often found in larger rays of the Compositae are anything other than corolline in nature. The fact that they stand out on the lower surface of the ray is more likely to be simply a matter of architectural engineering than something of profound phyletic significance. A consideration of the rays of *Gaillardia aristata* (Helenieae) might be instructive in this regard. Here *all* of the veins stand out on the lower surface of the ray, in the fashion of the two or three large veins of some of the genera of the Heliantheae and other tribes. Even if one takes the doctrine of vascular conservatism as the true gospel, it would require far less vascular modification to make the veins of the corolla stand out on the lower surface of the ray than to abort the vascular supply of the corolla and relace it by part of that of the calyx. Bizarre morphological conclusions based on floral anatomy are not as recent a phenomenon as one might suppose. As long ago as 1829 Don was led by the venation of the ray of *Zinnia* (Heliantheae) to conclude that instead of being a true corolla it is "an elongation of the exterior cortical layers of the ovarium."

With the supposed necessity to consider the two or three large veins as extra-corolline disposed of, one can reconsider the vascularization of the rays. The branching, disorganization, fusion, and rebranching noted by Dr. Koch in the lower part of the flower are so complex as to permit a wide variety of interpretations. Therefore no startling new conclusions should be drawn from the vascular anatomy alone. The two or three larger veins found in the larger rays of so many Compositae are reminiscent of the veins of the disk. Whether they are strictly homologous with the veins of the disk-corollas might be questioned but is far from disproved. Since the same genes which are present in the disk-corollas are also present in the rays, it should not be surprising to find similarities in vascularization, whether the comparable bundles are strictly homologous or merely analogous.

The lack of conformity of the venation of the ray and disk-corollas suggests that the derivation of the rays preceded the reduction and modification of the vascularization of the disk. It supports the hypothesis that the rays differentiated at a stage in the ancestry of the family when both central and lateral veins were present in the corolla-segments. Then in most of the family the reduction in vascularization of the rays proceeded more

or less conformably with that of the disk-corollas, while in some instances it took a contrary path, leading to the suppression of the lateral veins and retention of the central ones. The rays being very unstable in degree of development, and showing a strong tendency toward reduction and final suppression, their vascularization tends to be further reduced and eventually loses any clear relation to the 3 corolla-lobes involved in the ray.

As pointed out by Dr. Koch, the bilabiate flowers of the Mutisieae are clearly derived from normally veined disk-corollas, and there is nothing remarkable in their vascular anatomy. The tribe presents all transitions from disk-flowers, to bilabiate flowers, to normal rays involving 3 lobes of the corolla (but often with reduced vascularization), and the derivation of the mutisious ray from disk-corollas having the characteristic venation of the family seems well established. It is the variation in the Heliantheae, rather than in the other tribes, that suggests an ancient derivation of the ray-corolla from a tubular corolla with normal, unreduced venation.

The vascularization of both the ray and disk-corollas is thus wholly compatible with, and gives some support to the phyletic arrangement proposed in this paper.

Pigmentation of the corollas.—The color of the flowers has long been used as a taxonomic character in the Compositae, but less attention has been paid to the chemistry or to the possible phyletic significance of the pigmentation. There have not been enough analyses of the flower-pigments to permit a comprehensive integration of their chemistry into the taxonomy of the family at this time. Enough has been done to show that there is a great deal of variability, that the yellow pigments are partly plastid-borne carotinoids and partly water-soluble anthoxanthins chemically allied to the anthocyanins, and that several yellow pigments, including both carotinoids and anthoxanthins, may be present in a single flower.

A group of anthoxanthins which turn red when heated or when treated with mild alkali, and which give a rusty red to orange-red precipitate with stronger alkali, have been termed anthochlors. They have been found in nearly 200 species of the Coreopsidinae (Gertz, 1938; Geissman 1941a, 1941b, 1942; Geissman & Heaton 1943, 1944). Save for several species of *Baeria,* they are not known to occur elsewhere in the family. The fact that one of the anthochlors, butein, has also been found in a legume (Geissman, 1942) suggests that further studies may demonstrate their presence in other families as well, so that the significance of their occurrence, like other taxonomic feasures, must be evaluated with some caution. Within the Compositae, their very wide distribution in and usual restriction to the Coreopsidinae furnish further evidence of the naturalness of that subtribe.

The scarlet pigment found in the rays of some of the cultivated Dahlias has been considered by Lawrence (1929) to be an anthocyanin. When extracted by boiling in water it is visually similar to the water-extracted anthochlor of *Coreopsis grandiflora,* and it gives a similar precipitate when treated with KOH. It therefore seems probable that it is chemically closely allied to the anthochlors. Buxton and Darbyshire (1929) found that the anthocyanins of a number of flowers in various families did not all respond in the same fashion to changes in PH, with at least two general groups being indicated. Several chemical classes of anthocyanins have subsequently been recognized, and the interconvertability of certain

anthoxanthins with anthocyanins by minor chemical alteration has been demonstrated (Blank, 1947). Thus it appears that the division of the water-soluble pigments into anthocyanins and anthoxanthins is more convenient than chemically accurate.

At the present state of our knowledge, and especially in view of the fact (Gertz, 1938; Geissman, 1941a) that anthoxanthins and carotinoids may exist in the same flower, the correlation of pigmentation with the taxonomy and phylogeny of the Compositae must be done largely on the basis of the color rather than the chemistry of the pigments. This may not be so misleading as would at first appear, for although the important chemical step, presumably involving more genetic change, is from carotinoids to the water-soluble pigments, the important step from the standpoint of attraction of pollinators and thus of adaptation and survival-value, is from yellow or orange to the cyanic colors. Thus the larger chemical change can be accomplished with little or no effect on survival, while the important physical change can be accomplished by very minor genetic alteration. This holds true regardless of the direction of the change.

Considering first the radiate tribes as a group, one finds that yellow is by far the commonest color for both the ray and the disk-flowers. Only the Astereae have large numbers of cyanic-flowered species, and in that tribe there are numerous wholly xanthic species as well. Scattered species in the Heliantheae (e.g., *Helianthus* spp.) and elsewhere have a cyanic pigment superposed on the xanthic pigment(s) of the disk-flowers, giving the disk a dull reddish brown color. In other species (e.g., *Coreopsis* spp., *Gaillardia* spp.), the rays have a basal blotch of cyanic pigment covering the more generally distributed xanthic pigments(s). In still others (e.g., *Cosmos* spp.), the pigmentation of the rays, at least, is wholly cyanic. White-rayed species or forms may be found among both predominantly xanthic and predominantly cyanic groups.

Except among the Astereae, the species with wholly cyanic pigments in the rays and/or disk-flowers do not in general form natural groups larger than genera, and often they are merely individual species. Most of the genera of the Astereae have customarily been divided into two partly natural groups, the Homochromeae, with both the rays and the disk yellow, and the Heterochromeae, with the rays cyanic to white. Most of the Heterochromeae have xanthic disks contrasting with the cyanic rays (whence the name), but a fair number, notably numerous spp. of *Aster*, have both the rays and the disk cyanic, without yellow pigments. I find nothing to suggest that the wholly cyanic-flowered species of the Astereae are primitive in other features, and in *Aster* proper they are definitely among the more advanced species.

It seems to me that the most reasonable interpretation of these facts is that among the radiate tribes, xanthic flowers are primitive, and cyanic flowers derived. The process is apparently reversible, however, since the 4 yellow-rayed North American species of *Erigeron* seem to be derived in 2 independent lines from cyanic-rayed ancestors (Cronquist, 1947). Since the anthoxanthins are chemically allied to the anthocyanins, but often occur with the carotinoids, one may reasonably speculate that the general progression is from carotinoid to anthoxanthin to anthocyanin.

Going on to consider the other tribes, one finds that xanthic pigments

are dominant in the Cichorieae, frequent in the Mutisieae, uncommon in the Cynareae, and unknown in the Vernonieae and Eupatorieae. In the Cichorieae cyanic pigments appear to be secondary. There is nothing to suggest that the cyanic-flowered species of this tribe are primitive in other respects, nor do they form a natural group. Some of these cyanic pigments, such as the azure blue found in species of *Lactuca*, are probably closely allied chemically to the xanthic pigments, since the two colors may occur in the same species in such a way as to suggest that the difference is controlled by a single pair of genes. The rarity of this pure blue shade in angiosperm flowers further indicates that in this case the blue is probably derived from the yellow, rather than vice versa. The blue pigment found in the flowers of *Cichorium Intybus* is visually similar to that in the Lactucas just mentioned. It responds in the normal fashion of anthocyanins by turning red when treated with acid, but, unlike ordinary anthocyanins, it turns yellow when extracted in tap-water or when treated with KOH. Pending actual analysis, the very close relationship between some of the blue and some of the yellow pigments in the Cichorieae seems to be indicated.

The advanced position uniformly accorded the Cichorieae in taxonomic treatments is scarcely significant as to the evolution of flower-color, since, as pointed out elsewhere in this paper, the Cichorieae are probably derived from near the ancestral prototype of the family, rather than directly from the Mutisieae or any of the discoid tribes. The relatively primitive cichoriaceous genus *Dubyaea* includes both xanthic- and cyanic-flowered species, and *D. atropurpurea*, considered by Stebbins (1940) to be the most primitive in the genus, evidently has both types of pigments in the flowers. The evidence from the Cichorieae on evolution of flower-color, while less conclusive, is thus wholly in accord with that from the radiate tribes.

Among the Mutisieae, xanthic pigments are less common than cyanic ones, but yellow-flowered genera occur in all of the subtribes. Small (1918) considered the taxonomic position of the xanthic-flowered members of this tribe to support or at least be concomitant with the assumption that yellow is the primitive color for this tribe as for others. My own limited knowledge of the group does not disclose any indications as to which colors are the more primitive for the Mutisieae.

The Cynareae are predominantly cyanic, and the scattered distribution of the xanthic pigments indicates that for this tribe, at least, the cyanic colors are probably the more primitive. Since the evolutionary forces (whatever their nature) acting in the Compositae and other organisms are likely to affect related species and genera in similar fashion (parallelism) it is possible that the scattered yellow pigments found in the Cynareae represent individual survivals that escaped the general change to cyanic flowers in the tribe. The serious advancement of such a hypothesis must await further evidence. The more obvious explanation is that the cyanic colors are primitive for the tribe, and the few xanthic-flowered species are derived from cyanic-flowered ancestors within the tribe. Such a situation would not be incompatible with that described in the radiate tribes and in the Cichorieae, since evolutionary trends cannot be expected to be rigid and irreversible, and we have already noted that in *Erigeron* the xanthic species appear to be derived from the cyanic. The obviously

advanced taxonomic position of the Cynareae militates against the uncritical extension to the rest of the family of any conclusions drawn from this tribe alone as to trends in flower-color. It will be interesting to learn, however, whether the xanthic pigments in this tribe are wholly anthoxanthins, or whether some carotinoids are included.

The absence of xanthic pigments in the Vernonieae and Eupatorieae is of no great importance in establishing the primitive condition for the family, since these tribes are not primitive on other grounds. Their uniformly cyanic-flowered state could equally well be a survival of a primitive character or an advanced condition coherent with their morphological advancement. The fact that the only likely connecting form between the Vernonieae and the radiate tribes (*Gongrothamnus*) has yellow flowers may be significant, especially if one adopts the view here presented as to the relationships and evolution of the tribes.

The evidence from the discoid to ligulate tribes thus does not controvert the evidence from the radiate tribes as to the evolution of pigmentation in the flowers in the family. The flower-colors found in the Cichorieae, Mutisieae, Cynareae, Eupatorieae, and Vernonieae are compatible with the hypothesis, developed for the radiate tribes, that yellow is the primitive color of the family, that cyanic colors (and white) are derived, and that individual reversals of the trend occur.

The conclusions here reached as to evolution of flower color in the Compositae are in accord with those of Small (1918). He cites numerous contributions going as far back as 1879 which uniformly treat xanthic colors as being more primtive than cyanic colors for angiosperm flowers in general. Speaking of the Astereae, he says: "We then get the yellow Homochrominae giving the Heterochrominae with the higher colors appearing first in the rays and then spreading to the disk." He considers that the evidence from the other Compositae as well as the Astereae supports the general trends discovered by earlier authors. Hutchinson (1948) also considers yellow to be the primitive flower-color for the family.

Nature of the pappus.—The pappus has classically been considered to represent a modified calyx. This would seem an obvious interpretation, since it occupies the position of the calyx, which would otherwise be missing. The very pappus-like calyx of *Valeriana* in the Rubiales, and *Jasione*, in the Campanales, provides a further strong suggestion of the nature of the pappus, whichever of these two orders one considers the more nearly ancestral to the Compositae. Furthermore, it is a well known evolutionary principle that new structures are usually derived by modification of preexisting structures, rather than originating from nothing. This same principle is behind the dictum that *Organs do not arise functionless.*

Various authors have suggested that the true calyx is obsolete in the Compositae, and that the capillary pappus, in particular, represents merely a series of appendages to this obsolete calyx. (References and discussion are given by Small.) To my mind this is scarcely more than a play on words; if the appendages arise from the calyx (ontogenetically and phylogenetically) they are part of it, and reduction of the original organs would not negate the calycine nature of the appendages. An interpretation of the capillary pappus as appendicular is also unnecessary, since steps in the origin of a capillary pappus by longitudinal fission of the scales are well shown

in several genera of the Heliantheae such as *Dysodia*. Once the genetic tendency toward a capillary pappus is well established, the pappus may even be augmented by enlarging the uppermost hairs of the achene. The short outer pappus of some species of *Erigeron* (Cronquist, 1947) appears to have been derived in this fashion, while in other species of the same genus the same result is obtained by reducing some of the principal bristles. Thus, although in an evolutionary sense the pappus is a modified calyx, it may not always, in its more modified states, be strictly so in a morphological sense. The fact that its members cannot always be homologized with individual sepals does not negate its evolutionary origin. Primitively, the pappus should consist of 5 members, either free or partly connate.

Anthers.—Although the connation of the anthers so commonly found in the Compositae is obviously derived from the more general angiospermous condition in which the anthers are free, the evidence is that *within the family* the connate condition is primitive, and the free condition derived. Save for scattered small genera in other tribes, it is chiefly the subtribe Ambrosiinae of the Heliantheae which have free anthers. This subtribe, which has adopted wind-pollination with its so frequently attendant floral reduction, is so definitely advanced in floral morphology, and so clearly connected to other, more normal Heliantheae, that the lack of connation of their anthers can scarcely be considered to be primitive.

It seems unnecessary to defend the thesis that tailed anthers are derived from tail-less ones.

Style-branches.—There seems no good reason, in considering the style-branches, to depart from the evolutionary principle that the unspecialized precedes the specialized. The style-branches with well developed stigmatic lines could thus be derived from a type such as is seen in many of the Heliantheae, in which the style-branches are hispidulous throughout, with poorly or scarcely differentiated stigmatic portions that fade out distally. The style-branches found in some species of *Vernonia*, in which the whole inner surface of the branch appears to be stigmatic, might also be considered to be relatively primitive. The more common condition in *Vernonia* appears to be that described by Bentham; i.e., there are weakly differentiated ventromarginal stigmatic lines toward the base of the style-branches. These lines sometimes gradually disappear upwards; in other cases they stop rather abruptly, so that the style is not much different from some of the more narrowly and elongately appendiculate Astereae. In some species the stigmatic lines appear to continue nearly or quite to the apex, and there is more variability in the vernonious style than one might be led to believe from the descriptions, even though styles characteristic of the other tribes are not to my knowledge found within the group. It would not be surprising if in those Heliantheae and Vernonieae with weakly differentiated stigmatic lines there might be a possibility of successful germination of the pollen grains on parts of the branches that do not appear to be stigmatic.

The eupatorious style could be derived from the vernonious type of shortening and thickening the hairs into mere papillae, increasing slightly the morphologic differentiation of the stigmatic lines, and changing the form of the branches to slightly clavate.

The astereous style is readily derivable from the primitive heliantheous style by differentiation and restriction of the stigmatic lines, leaving a

sterile, hairy, terminal appendage. All the intermediate stages can in fact be observed in the Heliantheae, some genera of which have styles that could readily pass for those of he Astereae.

The anthemideous or senecioneous style differs from the astereous style in being truncate, exappendiculate, and penicillate. It seems to be a result of reducing the appendage but retaining the hairs. Intermediate styles, with the branches very shortly appendiculate, are observable both in the Heliantheae and the Senecioneae. It should be noted that the term astereous style is used to describe a morphological form which exists to a limited extent in the Heliantheae as well as in the Astereae, and that neither the Senecioneae nor the Anthemideae have been derived from the Astereae.

The inuleous style has smooth or papillate branches which are either truncate or rounded; in the latter case, the stigmatic lines are confluent at the tip. This type of style is again derivable from the primitive heliantheous type, by differentiation and restriction of the stigmatic areas, and reduction of the hairs to papillae.

The arctotidean and cynareous styles, with the branches papillate and more or less connate, and with a more or less abrupt change of texture below the branches, are more highly modified than those of the other tribes. Morphologically, these might be derivable from the inuleous style by connation of the branches and by adding the abrupt change of texture. On other grounds, however, there seems no very good reason to juxtapose the Inuleae to the Arctotideae and Cynareae. A stage similar to that now found in the Inuleae may have been included in the derivation of the cynareous style from the primitive heliantheous style, but if so it probably represents another case of parallelism.

The Mutisieae have highly diverse style-branches, presenting forms varying from that of the Cynareae to nearly or quite as in the Inuleae and Senecioneae. So far as I am aware no styles found in the Mutisieae approach the primitive heliantheous style.

The Cichorieae are so well marked by other characters that little attention is paid to their styles. These are elongate, generally smooth or nearly so, exappendiculate, and either with ventromarginal stigmatic lines extending to the tip or apparently wholly stigmatic within. *Dubyaea,* considered by Stebbins (1940) to be the most primitive surviving genus of the tribe, has the branches hispidulous on the outside, and apparently wholly stigmatic within, thus approaching a type found in the Vernonieae. Pistillate flowers, in whatever tribe, commonly have styles much like those of the Cichorieae. It is largely in the disk-flowers that the different characteristic style-branches occur. The styles of sterile (functionally staminate) disk-flowers, in whatever tribe, tend to become more or less connate and to lose their distinctive features, so that it is only the fertile disk-flowers which can be expected to have the styles characteristic of their tribe.

Since much of the modification of the style-branches of the Compositae is obviously correlated with their function in ejecting the pollen, one might seek some hints as to the primitive condition from the styles of the rays, particularly if the suggestion made in this paper is correct that the rays differentiated early in the origin of the family. These are disappointing, however, since as noted above they resemble only the styles of the Cichorieae, the ray-flowers of which are 5-toothed and have a differ-

ent origin. Otherwise the nearest comparison is between some rays with the whole inner surface of the style-branches apparently stigmatic and the styles of some species of *Vernonia* which also have the whole inner surface apparently stigmatic. One cannot exclude the possibility that this condition, rather than the absence of a well differentiated and sharply limited stigmatic region on the style-branches is the primitive one. If so, it would be the sole feature, in my opinion, in which the Vernonieae (or some of them) are more primitive than the Heliantheae.

Having considered the primitive characters within the family, we may proceed to consider which tribe most nearly fills the requirements. A plant which showed all the primitive features listed above would surely be put in the Heliantheae. Since the primitiveness of the opposite-leaved condition is established partly by the argument that opposite leaves are characteristic of the primitive tribe Heliantheae, this character might perhaps be excluded from consideration at the moment. A plant having alternate leaves, but being primitive in all the other respects discussed, would still be put in the Heliantheae. Since some doubt might be cast on the primitiveness of the radiate condition, this character too may be excluded from consideration for the moment. A discoid, alternate-leaved plant, primitive in the other characters under consideration, would still be placed in the Heliantheae (witness *Marshallia,* which also has cyanic rather than xanthic flowers). The other radiate tribes are in general related to each other through the Heliantheae. Although the discoid tribes stand apart as a group from the Heliantheae and the other radiate tribes, each of the discoid tribes is relatively primitive in some features and advanced in others, so that they are related to each other only through a common ancestor which could not be placed in any of the presently known discoid tribes. A plant which combined all the primitive features found in individual genera or species of the discoid tribes would be most nearly at home in the Heliantheae. The conclusion is inescapable that the Heliantheae represent the most primitive tribe of the Compositae.

No one genus of the Heliantheae is primitive in all characteristics Some species of *Wyethia* have attracted attention for their primitiveness, but in this genus the leaves are alternate. *Wyethia* therefore cannot be considered to represent the true prototype of the family, but its ensemble of primitive features, quoted by Weber (1946) from a letter by Stebbins, is worthy of repetition:

> "The inflorescence of these species, consisting of a few heads on stout peduncles coming from the axils of leaves rather than bracts represents the most primitive type of inflorescence in any group. The involucral bracts are more leaf-like, and pass more gradually into the upper cauline leaves, than in any other composite. Also the receptacular paleae are more bract-like than in any other composite, and there is great similarity between inner involucral bracts and the outer row of receptacular paleae. This may all be summed up by saying that the transition from the lowermost to the uppermost of the subtending foliar organs is more gradual, and the serial homology between them is more evident in these *Wyethia* species than in any other members of the family known to me.
>
> "Next, *Wyethia* is one of the very few genera of the primitive tribe Heliantheae in which all of the florets are fertile and in which all of the floral parts: namely, calyx, corolla, stamens, and gynoecium, are present in all of the disk florets. Next, the ovary is large at flowering time as well as in the achene, and is not modified by flattening. Furthermore, the ovary cavity at anthesis is relatively large, so that the ovule is far from

filling it, and in *W. helenioides* I have not infrequently found two ovules per ovary. Then, the pappus is more calyx-like than in any other composite known to me.

"Finally, the vascular anatomy of the florets is complex and highly developed. The midvein of the corolla-lobe is present, as well as the fused laterals; the lateral bundles of the style are sometimes present, as in species of *Dubyaea*.

"These points tie in with the distributional pattern . . . to give a general picture of primitiveness that is approached only by a few genera of the Mutisieae, which have an obviously specialized setose pappus and lack receptacular paleae; perhaps in some Vernonieae; and in the primitive Cichorieae . . . which are in several respects more advanced than in *Wyethia*."

Stebbins (1939) has noted that *Palaeanthus problematicus* Newberry, from Upper Cretaceous deposits in New Jersey, resemble a *Wyethia*. Newberry's (1896) drawings show several detached heads in various stages of fragmentation. I agree with Gray (as quoted by Newberry) that it is a Composite, and with Newberry that it resembles the Heliantheae. I do not think any more definite identification is warranted by the material. The fairly numerous other fossils which have been referred to the Compositae, are all, so far as I am aware, more recent, being mostly from Oligocene and later deposits. A large proportion of them are based on achenes with or without an apparent pappus, or even on mere leaf-impressions, so that the identifications are subject to some question. Since even the best of the pre-Pleistocene fossil Compositae are only with difficulty if at all referable to a tribe, it is evident that no assistance as to the phylogeny of the family is provided by the fossils now known.

One of the most striking features of evolution within the Compositae is parallelism. The same or similar developments occur repeatedly, independently, in diverse species, genera, and tribes. The tangled pattern of apparent relationships within the family is doubtless due to the difficulty of distinguishing between similarities due to common descent and similarities due to parallelism. The supposed relationship of the Inuleae to the Astereae, through the disciform types with numerous slender, tubular, pistillate marginal corollas, is thus illusory, since the genera involved can be shown to have developed from normal radiate ancestors within their respective tribes.

A large proportion of the evolutionary trends, or tendencies, operating in the Compositae can be grouped under the heading of aggregation and reduction. This has been implied by Bentham, specifically so stated by Small (1918), and accepted without published dissent by other synantherologists in general. Small considered that natural selection was insufficient to explain these tendencies, since "The development along these lines has proceeded under the pressure of orthogenesis beyond the limit of efficiency in quite a number of Composites." I have elsewhere expressed a similar opinion (1951), but regardless of the mechanism, the tendencies exist. In the involucre, they are expressed by loss of herbaceousness of the bracts, and by their reduction to a single series, the two expressions of the trend proceeding more or less independently. In one genus, *Psilocarphus*, the involucre has been lost entirely. In the ray-corollas, the tendency toward reduction is expressed in three ways: by simple abortion of the ligule, leaving the tubular base of the corolla intact; by the abortion at a single step of the whole pistillate flower; and by the attenuation and elongation of the tube with concomitant reduction of the ligule. This last type of re-

duction often marks genera or groups of genera, as in the Astereae, Inuleae, and Senecioneae, while the two former types are more sporadic and sometimes fail even to mark species.

The number of flowers in each head tends to decrease evolutionarily, reaching the ultimate limit of one in diverse genera in most of the tribes. The reduction in number of flowers is often accompanied by an increase in number and an aggregation of the heads, so that in several tribes there are genera with 1-flowered heads, each with its own involucre, aggregated into a separately involucrate secondary head. In some species of *Psilocarphus* (Cronquist, 1950) we have an aggregation of the heads without much reduction in number of flowers, resulting in a lobed receptacle, each lobe bearing its central cluster of staminate flowers surrounded by several series of pistillate flowers (The genus has no involucre).

Other expressions of the trends toward aggregation and reduction are indicated in the discussion of the individual primitive characters. It should be noted that these as well as other trends are not irreversible, and Stebbins (1950) has noted the existence of an enlargement series in the Cichorieae culminating in the genus *Tragopogon*. For a longer discussion of the evolutionary trends in the family and the mechanisms which might bring them about, the reader is referred to my cited paper of 1951.

A consideration of the relationships among the tribes might well be preceded by a conspectus of the tribes, which follows.

CONSPECTUS OF THE TRIBES OF THE COMPOSITAE

1. Heads radiate (i.e., with the central flowers perfect or functionally staminate, with regular, tubular corolla; and the marginal flowers pistillate or neutral, with 3 corolla-lobes prolonged into a strap-shaped ligule above the short tubular base, the other 2 corolla-lobes obsolete or nearly so), or disciform (i.e., the corollas of the pistillate flowers slender and tubular, without a ligule), or discoid (i.e., the flowers all perfect, with regular, tubular corolla), or with some of the flowers bilabiate, but never (save in a few anomalous Mutisieae) ligulate; plants mostly with well developed resin-ducts and without latex; latex, if present, almost always (exceptions: *Gundelia, Gazania, Warionia*) in isolated cells or pockets rather than in a system of anastomosing canals; pollen-grains[1] lophate with 30 or more lacunae, or more often non-lophate, not appearing angular; leaves, involucre, and pigmentation various.

2. Heads chiefly radiate, or not infrequently disciform, or in scattered genera, species, and individuals discoid[2]; predominant color of corollas yellow, although various cyanic shades and white are not uncommon; pollen spiny, or, especially in wind-pollinated groups, smooth or nearly so, not known to be lophate save in *Berkheya* of the Arctotideae.

3. Lower (or all) the leaves tending to be opposite, although a number of genera have wholly alternate leaves; pappus chaffy, or of a few firm awns, or none, rarely subcapillary; receptacle chaffy in most genera, less often naked; involucral bracts tending to be herbaceous and several-seriate, but varying in groups of genera to uniseriate, or subchartaceous, or even concrescent into a bur; style-branches more or less hispidulous and with the stigmatic lines poorly defined, varying to as in the Astereae or Anthemideae; anthers basally obtuse to sagittate, scarcely caudate; rays tending to be relatively broad, often much larger than is usual for the other tribes; pollen grains, save in the wind-pollinated genera, mostly with long, slender spines ..... 1. *Helianthеae*

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1 The data on pollen-morphology are taken from the several cited papers of Wodehouse, and are subject to modification as more information becomes available.

2 A few discoid species or genera have the corollas of the marginal flowers irregular and more or less ampliate, recalling to some degree the bilabiate corollas of the Mutisieae.

3. Leaves all alternate, except in scattered genera (notably *Arnica* and *Liabum*, of the Senecioneae); involucre, receptacle, pappus, and anthers various; stigmatic lines mostly evident and well defined; pollen grains mostly with relatively short spines.
   4. Involucral bracts mostly in several series, imbricate or subequal (or the outer larger), rarely equal and uniseriate, or even wanting; calyculus wanting; receptacle, pappus, anthers, and styles various.
      5. Anthers obtuse to strongly sagittate, rarely subcaudate; styles diverse, but mostly not as in the following group; pappus and receptacle various; heads discoid, disciform, or more often radiate, the rays either xanthic like the disk (homochromous) or cyanic to white (heterochromous).
         6. Style-branches discrete, flattened, with marginal stigmatic lines, ordinarily either penicillate or with minutely hairy appendages; plants not spiny.
            7. Involucral bracts herbaceous to chartaceous, rarely evidently hyaline-scarious toward the margins and tip; receptacle naked, or rarely with deciduous chaff; style-branches nearly always appendiculate; pappus capillary, chaffy, or occasionally none; leaves usually entire or merely toothed, rarely dissected; plants mostly inodorous, or in any case not with the characteristic odor of the following group; pollen grains with the surface between the spines only finely granular or nearly smooth ..... 2. *Astereae*
            7. Involucral bracts mostly rather dry and scarcely herbaceous, becoming hyaline-scarious toward the margins and tip; receptacle chaffy or naked; style-branches mostly truncate and penicillate; pappus none, or minute and chaffy or coroniform; leaves mostly more or less dissected, varying to sometimes entire and then mostly small; plants mostly with a characteristic odor; pollen grains with the surface between the spines conspicuously and coarsely granular ..... 3. *Anthemideae*
         6. Style-branches generally connate to near the tip, papillate, the style abruptly or more gradually thickened and changing in texture at or slightly below the base of the branches (style of *Ursinia* similar to that of the Anthemideae); plants not infrequently with the involucre or leaves more or less spiny; pappus chaffy or none; receptacle naked or sometimes chaffy ..... 4. *Arctotideae*
      5. Anthers more or less strongly caudate at the base, rarely merely sagittate; style-branches flattened, with marginal stigmatic lines, generally glabrous or merely papillate, and either subtruncate or broadly rounded at the tip, the stigmatic lines in the latter case confluent, varying, rarely to essentially as in the Astereae or Anthemideae; pappus mostly capillary, rarely chaffy or none; receptacle chaffy or naked; heads very often disciform or discoid; rays when present generally yellow like the disk ..... 5. *Inuleae*
   4. Involucral bracts mostly equal and subuniseriate (save in *Liabum* and a few small genera); calyculus of very much reduced bracts often present; style-branches flattened, with marginal stigmatic lines, typically truncate, exappendiculate, and penicillate, varying to rarely as in the Vernonieae, Eupatorieae, Astereae, or Inuleae; anthers mostly sagittate at the base, or in some of the Calenduleae shortly caudate; receptacle naked, rarely bristly or chaffy; pappus capillary (sometimes plumose) or none.
      5. Pappus well developed, or rarely absent; achenes mostly all alike; widespread ..... 6. *Senecioneae*
      5. Pappus wanting, or rarely present but poorly developed; achenes mostly heteromorphic; Africa ..... 7. *Calenduleae*

2. Heads discoid, or with some of the corollas bilabiate; pollen and pigmentation diverse.
   3. Anthers obtuse to sagittate at the base, rarely subcaudate; heads ordinarily strictly discoid, with regular, tubular corollas; plants not spiny; corollas cyanic to sometimes white, or rarely (notably in spp. of *Mikania*) ochroleucous, never truly yellow; receptacle naked or rarely chaffy.
      4. Style-branches obtuse and often more or less clavate, minutely papillate, not

hairy; anthers obtuse or rarely sagittate at the base; leaves mostly opposite, varying to sometimes alternate or whorled; pollen grains minutely spiny, not at all lophate ..... 8. *Eupatorieae*

4. Style-branches gradually attenuate, minutely hispidulous outside; anthers more or less strongly sagittate or rarely subcaudate; leaves nearly always alternate; pollen grains lophate, with 30 or more lacunae, the ridges usually spiny ..... 9. *Vernonieae*

3. Anthers more or less strongly caudate, rarely merely sagittate; plants often (especially the Cynareae) with the leaves or involucre more or less spiny; leaves alternate or rarely opposite; styles various, but scarcely as in either of the two foregoing tribes; corolla cyanic, or not infrequently xanthic, or occasionally white; receptacle various.

4. Heads usually strictly discoid, the corollas slightly if at all irregular (marginal flowers pistillate or neutral and irregularly subradiate in a few genera); style with a thickened, often hairy ring below the branches, changing abruptly in texture at that point and papillate thence to the tip, the branches commonly, more or less connate at least below; receptacle mostly bristly, sometimes chaffy, rarely naked; pollen grains spiny to smooth, not lophate.....10. *Cynareae*

4. Heads generally with some or all of the corollas bilabiate; corollas, if all regular, deeply lobed; style various, often much like the Cynareae; receptacle naked or rarely chaffy; pollen grains spiny to smooth, or in *Barnadesia* lophate and spineless ..... 11. *Mutisieae*

1. Heads ligulate (the flowers all perfect and with a ligule derived from all 5 lobes of the corolla); plants with latex in a more or less well developed system of anastomosing canals, without resin-ducts, or rarely (*Scolymus, Scorzonera*) with resin-ducts in the roots; pollen-grains, except in a few genera, lophate (i.e., with polygonal lacunae enclosed by definite ridges) with spiny ridges, the lacunae mostly 6-21, the grain appearing angular; involucral bracts tending to be subequal in 1-2 series, often calyculate at the base, less often imbricate in several series; leaves alternate (or all basal) or rarely opposite; predominant color of corollas yellow, although various cyanic shades and even white occur ..... 12. *Cichorieae*

As already noted, the Heliantheae are the most primitive tribe of the Compositae. Even if the discoid condition is eventually confirmed to be more primitive within the family than the radiate condition, the Heliantheae cannot be excluded from consideration as the basal group. Such discoid heliantheous genera as *Marshallia,* which appears to be without close relatives, show no direct evidence of a radiate ancestry. *Marshallia* is further interesting because of some resemblances to the Vernonieae. Unlike most of the Heliantheae, it has strictly cyanic flowers, as in the Vernonieae. The leaves are wholly alternate, as in the Vernonieae, rather than partly opposite, as in most Heliantheae. The deeply lobed corollas find their closest match in some of the Mutisieae, although a similar condition is not unknown in the Vernonieae and Eupatorieae. There is no question of transferring *Marshallia* to any of the discoid tribes, where it has no close relatives and where its style would make it anomalous, but the suggestion afforded of a connection between the discoid and radiate tribes should not be overlooked. The seemingly much closer connection between the Arctotideae (radiate) and the Cynareae (discoid) loses some of its force because neither of these two tribes can on morphological grounds be considered to be primitive. Another possible link between the discoid and radiate tribes, *Gongrothamnus,* is discussed elsewhere in this paper.

One of the evolutionary developments that has taken place repeatedly within the Compositae is loss of chaff from the receptacle. The usual presence of well developed chaff is one of the features of the Heliantheae

which have caused Bentham, myself, and doubtless others to consider them primitive. Both the Inuleae and the Anthemideae appear to have inherited the chaffy receptacles of their more primitive members from the Heliantheae, and the loss of chaff in these two tribes has proceeded independently, probably occurring more than once in each tribe. The nearly uniformly naked condition of the receptacle in the Senecioneae and Astereae appears likewise to have been independently derived in each case. All of these tribes, like so many natural groups, are defined on a tendency toward concordance of several independently fluctuating characters or evolutionary trends.

Unlike the other tribes of the Compositae, the Helenieae have customarily been distinguished from their nearest relatives, the Heliantheae, by a single technical character: the presence or absence of chaff on the receptacle. And here, as in so many other cases in which taxonomic groups have been established on a single technical character, the resulting division is artificial. The several subtribes of the Helenieae appear to have been independently derived from the Heliantheae. The connection between *Gaillardia,* of the Helenieae-Heleninae (which furthermore has a generally bristly rather than naked receptacle) and *Rudbeckia,* of the Heliantheae-Verbesininae, is obvious. The Helenieae-Baeriinae, on the other hand, find their closest relatives among the Helentheae-Madiinae, although the relationship is not linear. In addition to some resemblances in involucre and habit, these two subtribes of supposedly different tribes are connected by a genus of doubtful position, *Rigiopappus. Rigiopappus* has customarily been included in the Baeriinae, but, as H. L. Mason has noted on some herbarium labels, it has a row of marginal receptacular bracts (internal to the rays) as in the Madiinae. Save for the technical character of the partly bracteate receptacle, *Rigiopappus* would not be anomalous in the Baeriinae, yet to my mind it also recalls the Madiinae, which it technically resembles in its marginally bracteate receptacle. The involucral bracts merely half-clasp the marginal achenes, rather than enclosing them, but *Hemizonia,* which is regularly admited to the Madiinae, has this characteristic feature of the subtribe scarcely better developed. For want of a better position I have included *Rigiopappus* in the Madiinae in a floristic work now in preparation, but Dr. D. D. Keck, whose understanding of the Madiinae is well known, tells me that he thinks *Rigiopappus* should be excluded from that group.

The close resemblance of *Cacosmia* and *Geissopappus,* of the Helenieae-Jaumeinae, to *Calea* and *Galinsoga,* of the Heliantheae-Galinsoginae, has been pointed out by Bentham.

Both the Heliantheae and the Helenieae are essentially American in distribution, the Helenieae more strictly so than the Heliantheae. Thus we see that the Helenieae, which are similar to the Heliantheae in general appearance and geographical distribution, and which are separated from the Heliantheae solely by the technical character of chaffy versus naked receptacle, do not form a natural group, but are instead derived from the Heliantheae in several different lines. The Helenieae should therefore not be considered as a separate tribe; their subtribes should instead be inserted individually in the Heliantheae. This causes no difficulty in the classification of the rest of the tribes, which are in general natural groups.

It is interesting to note that the Helenieae were retained in the Heliantheae by Cassini (1826), and that later (1829, 1834), when he elevated the Tagetinae to tribal status, he still retained the rest of the Helenieae with the Heliantheae. He did not use the presence or absence of chaff on the receptacle even to define the subtribes of the Heliantheae. More recently, Leonhardt (1949) has also suggested that the Helenieae might better be submerged in the Heliantheae.

One of the subtribes of the Heliantheae, the Ambrosiinae, has become adapted to wind-pollination, and differs from the rest of the family in its much reduced corollas and free or nearly free anthers. This group might with some justification be considered to represent a separate tribe or even a separate family, as was done by N. L. Britton and his followers, and by many earlier authors as well. However, the Melampodinae furnish such a good series of transitional forms between the more normal heliantheous type and the less modified genera (such as *Iva*) of the Ambrosiinae that no serious criticism can be attached to the more customary treatment in which this small group of only 8 genera is considered to belong to the Heliantheae. In this connection it is worth noting that Wodehouse (1928b, 1935, 1945) considers the evidence from pollen-morphology and immunological reactions to confirm the relationship indicated by the traditional taxonomic characters.

The Senecioneae are defined principally by their uniseriate or sub-uniseriate (often also calyculate) involucre, and capillary pappus. Most of the genera have the style of *Senecio*, but variations approaching the Astereae, Vernonieae, Eupatorieae, and Inuleae occur. The monotypic genus *Dimeresia*, which on the basis of its involucres, anthers, and probable affinities belongs to the Senecioneae, has customarily been put in the Inuleae because of its fully inuleous style. The moderately large genus *Liabum*, which is anomalous in its vernonioid styles and its several-seriate involucre, was put in the Senecioneae by Bentham, and has been kept there by subsequent authors, partly because of its apparent relationship to such more definitely senecioneous genera as *Neurolaena* and *Schistocarpus*, and partly because it doesn't fit anywhere else. No genera are known to me to be so intermediate between the Heliantheae and Senecioneae as to be of doubtful position, but several genera of the Senecioneae show characteristics reminiscent of the Heliantheae. The opposite leaves of *Liabum*, *Allendaea*, *Schistocarpha*, and *Arnica*, the chaffy receptacle of *Allendaea*, *Schistocarpha*, and *Neurolaena*, and the very large rays of *Arnica* all recall the Heliantheae. These are primitive features, and if one put together all of the primitive features found in various genera of the Senecioneae one would have a plant separable from typical Heliantheae only by its capillary rather than chaffy pappus. Since a capillary pappus is also a derived feature within the family, the relationship of the Senecioneae to the Heliantheae seems established.

Even the vernonioid style of *Liabum* and its allies is compatible with a heliantheous ancestry, since the vernonioid style, with its poorly marked stigmatic lines and uniformly hispidulous outer surface, should on theoretical grounds be fairly readily derived from the style of some of the more primitive Heliantheae. The yellow flowers, and mostly opposite leaves and radiate heads of the Liabinae do not seem to favor a close relationship

with the Vernonieae. A possible connecting form is furnished, however, by the alternate-leaved, discoid, yellow-flowered genus *Gongrothamnus*, which was put with the Liabinae by Bentham, and submerged in Vernonia by Hoffman. Since it is considered in this paper that the ancestors of the Vernonieae had yellow flowers, opposite leaves, and radiate heads, the suggestion of a connection to the Liabinae through *Gongrothamnus* should not be too lightly discarded. Since the Liabinae themselves form a transitional group between the Heliantheae and more typical Senecioneae, the pattern formed by the apparent derivation of most of the other tribes directly from the Heliantheae would not thereby be seriously disturbed.

The close relationship of the Calenduleae to the Senecioneae has been pointed out by Bentham. All of the features in which the Calenduleae differ from the Senecioneae (heteromorphic achenes, absence of pappus, greater tendency toward subcaudate anthers) are advanced characters, and none of them furnishes an absolute technical character for the distinction. The general absence of a pappus in the Calenduleae does not of itself show that the pappus of their ancestors was capillary as in the Senecioneae; this is established instead by the existence of a fragile and caducous capillary pappus in the calenduleous genus *Dipterocome*.

The Inuleae are related to the Heliantheae through the inuleous subtribe Bupthalmeinae, which have chaffy receptacles, mostly well developed rays, and mostly chaffy pappus, combined with the technical characters of styles and anthers of the Inuleae. The relationship was duly noted by Bentham. Here again there are no actually doubtful genera, but an individual which combined all the primitive characters found in the Inuleae would scarcely be separable from the Heliantheae, and the similarity of *Anisopappus africanus* (Bupthalmeinae) to some species of *Verbesina* is striking.

Those whose chief familiarity with the Inuleae comes from the subtribe Gnaphaliinae and the genus *Inula* (which is introduced in North America) might be forgiven for questioning the naturalness of the tribe Inuleae. The African subtribe Relhaniinae, which varies from radiate to subdisciform (minutely radiate) to discoid, and which tends to have the involucral bracts scarious toward the tip, seems to furnish an adequate bridge between the two extremes. Bentham has pointed out that some of discoid Relhaniinae might nearly as well be placed in the Helichrysum group of the Gnaphaliinae. The tendency toward scarious-tipped bracts is also shown by the monotypic African genus Ondetia, of the primitive subtribe Bupthalmeinae.

There is sometimes a strong similarity in habit and general structure of the heads between members of the Inuleae-Plucheinae and genera of the *Conyza-Baccharis* group of the Astereae. The technical differences of styles and anthers generally remain fully developed, however, and I believe the similarity is due to parallelism rather than to a close relationship between the genera of the two tribes. Two small African genera may be an exception to the general condition. *Adelostigma* and *Gymnarrhena* have merely sagittate anthers, as in the Astereae. Their disk-flowers are sterile, so that no information as to their affinity can be gained from the style-branches. *Adelostigma* approaches the Inuleae in habit and involucre, but appears to be without close relatives in either group. It has been put in

the Astereae by Bentham and Hoffman. *Gymnarrhena* appears to be allied to *Geigeria*, of the Inuleae, because of which it has been placed in the Inuleae.

The Astereae are distinguished from the Heliantheae by the concurrence of several characters which are individually uncommon in the Heliantheae, and by the existence of a capillary pappus (a feature unknown in the Heliantheae) in a large percentage of the genera. The alternate leaves of the Astereae can be matched in numerous Heliantheae. The naked receptacle of the Astereae is found in the several subtribes of the Heliantheae that have been segregated as the Helenieae. The characteristic style of the Astereae is approached by many and matched by a few of the Heliantheae. Many of the Astereae have a chaffy pappus as in the Heliantheae. (It should be noted in this regard that at least some of the Astereae with chaffy pappus seem to have been derived from ancestors with capillary pappus, notwithstanding the fact that for the family as a whole the process seems to have gone in the other direction.) A much larger percentage of the Astereae have cyanic (or white) rays than do the Heliantheae, and none of the Astereae have the very large, firm rays so often found in the Heliantheae. The South African genus *Amellus*, with opposite leaves and chaffy receptacle, differs from the Heliantheae chiefly in its capillary pappus and cyanic rays. Steyermark (1937) has suggested that *Grindelia* might be allied to the Heliantheae, but it finds no close relatives there, while it is clearly linked to *Haplopappus* (Astereae) through *H. ciliatus*. The characters in which the Astereae differ from the Heliantheae represent evolutionary advances, and Steyermark's suggestion of a heliantheous relationship for the tribe seems well warranted.

Although the Anthemideae are placed next to the Astereae in the synopsis here presented, neither of these groups could have been derived from the other. The leafy involucral bracts of the basal species of *Aster*, *Erigeron*, and *Haplopappus* are more primitive, and more helianthoid than anything in the Anthemideae. On the other hand, many of the Anthemideae have well developed receptacular bracts, and are in that feature closer to the primitive Heliantheae than are the Astereae. The characteristic odor of the Anthemideae finds its nearest (though not exact) counterpart in the tendency of many of the Heliantheae to be odorous. The pappus of the Anthemideae is characteristically much reduced or obsolete, and is never capillary. The leaves of the Anthemideae are usually more or less dissected, while those of the Astereae (and Heliantheae) are seldom more than merely toothed. Thus we see that the Anthemideae and Astereae present different groups of phyletic advances from the Heliantheae, and are related to each other only through the Heliantheae. The same situation seems to be true in comparing any two of the tribes Senecioneae, Inuleae, Astereae, and Anthemideae. In a few cases small doubtful genera exist, but these are more likely to be a result of parallelism or convergence than of close relationship. In taking any two of these tribes, or sometimes even within a tribe, a combination in one individual of the primitive characters occurring in diverse genera would yield a plant scarcely or not all to be distinguished from the Heliantheae.

The Arctotideae are unmistakably related to the Cynareae. Except for the perhaps better excluded genus *Ursinia*, they share or approach the characteristic style of the Cynareae, which is not found in any of the other

radiate tribes. Several of the genera have the involucre, or the herbage or both more or less spiny, and some of the discoid species of *Berkheya* are kept out of the Cynareae chiefly because of their evident relationship to the radiate species of *Berkheya,* these latter belonging clearly to the Arctotideae. The discoid genera *Gundelia* and *Platycarpha* form another connecting link between the two tribes (as was indicated by Bentham), being retained in the Arctotideae chiefly because of their basally obtuse rather than caudate anthers. On the other hand, there is nothing save the style to separate the Arctotideae from the other radiate tribes. A number of species of *Arctotis* (sens. lat.) have scarious-tipped and-margined bracts, recalling the Anthemideae, and if Bentham is to be followed in placing *Ursinia* in the Arctotideae near *Arctotis,* no consistent differences are left between the Arctotideae as a whole and the Anthemideae. Hoffman, while pointing out the anthemideous habit and style of *Ursinia,* retained the genus in the Arctotideae, partly because of its well developed pappus. Even if *Ursinia* is transferred to the Anthemideae (where it would still be anomalous and without apparent close relatives), the very fact that so keen a student as Bentham was led to put it in the Arctotideae bears witness to the relationship between the two tribes.

The relationship of the Arctotideae to the Cynareae is particularly important because it demonstrates a connection between the discoid and the radiate tribes. The scarcely less firmly established relationship of the Arctotideae to the Anthemideae, as well as the general structure of the heads and predominantly yellow color of the rays, foredoom any attempt to divorce the Arctotideae from the other radiate tribes.

As has been indicated above, the Cynareae are allied to the Arctotideae. The Cynareae are also allied to the Mutisieae, and less closely to the Vernonieae. The connection to the Vernonieae is suggested by *Saussurea,* which although it has the styles and anthers unmistakably of the Cynareae, resembles species of *Vernonia* in habit and involucre. The receptacle of *Saussurea* varies from bristly, as in most Cynareae, to naked as in the Vernonieae. The stronger connection of the Cynareae to the Mutisieae has been pointed out by Bentham and by Hoffman. Save for the quite different Inuleae, it is only the Cynareae and Mutisieae which characteristically have caudate anthers. The shortly 2-lobed, glabrous or merely papillate styles found in a large proportion of the Mutisieae approach, if they seldom match, the typical cynareous style. Numerous species of *Cirsium* as well as other genera of the Cynareae have slightly irregular disk-corollas, with some of the sinuses deeper than others, thus showing a beginning of the tendency toward bilabiate corollas which in a stronger form marks most of the Mutisieae. Many of the Mutisieae have more or less spiny leaves or phyllaries as in the Cynareae. Finally, such genera as *Berardia, Warionia, Wunderlichia,* and *Atractylis* present various combinations of the usual characters of the two tribes. The first two of these were put in the Cynareae by Bentham (who recognized also their resemblance to the Mutisieae) and in the Mutisieae by Hoffman. *Wunderlichia* is generally considered to belong to the Mutisieae, but has setaceous-bracteate receptacles as in the Cynareae. *Atractylis* is commonly placed in the Cynareae, but some of the species have marginal flowers with 5-toothed ligules and abortive but

evident stamens, thus presenting a type of flower otherwise chiefly confined to the Mutisieae.

The pollen grains of the Mutisieae are unusually variable. (Wodehouse 1928c, 1929a, 1929b). The anomalous genus *Wunderlichia* has pollen like that of the Cynareae. *Barnadesia* has lophate grains much as in the Vernonieae, but the details of their structure indicate an origin from an essentially spineless ancestor. *Schlechtendahlia,* which Bentham segregated with *Barnadesia* into a separate subtribe of only 2 genera, has pollen grains which diverge from those of *Chuquiragua* (Gochnatiinae) in the direction of those of *Barnadesia.* The Nassauvinae have wholly spineless, deeply furrowed grains unlike anything else in the family, but *Lycoseris* and *Chaptalia,* of the Gerberinae, diverge in that direction from the commonest type in the tribe. Most of the genera of the tribe have pollen-grains more or less resembling those of the Cynareae, but with a more pronounced tendency toward reduction of the spines. Wodehouse (1929b) concluded that the Mutisieae are an un-natural tribe, mostly related (but presumably in separate lines) to the Cynareae, but with *Barnadesia* related to the Vernonieae. I do not believe his data warrant the transfer of *Barnadesia* to the Vernonieae, nor the conclusion that the remainder of the tribe is un-natural. They are in my opinion wholly compatible with the thesis here advanced that the Mutisieae are a natural tribe, allied to the Cynareae and less closely to the Vernonieae and Cichorieae. The resemblance of the pollen of *Barnadesia* to that of the Vernonieae is best considered an example of parallelism, since Wodehouse himself points out that the details of structure indicate an essentially spineless ancestor for Barnadesia, and spiny-grained ancestors for the lophate grains of the Vernonieae. *Barnadesia* would furthermore be anomalous in the Vernonieae both in its styles and in its corollas.

The Mutisieae are particularly interesting for the variety of their corollas. About a dozen genera have the flowers all perfect, with tubular, deeply but essentially regular 5-lobed corollas, which, except for the length of the lobes, are similar to the disk-corollas found in the other tribes. The other genera have some or all of the corollas irregular (mostly more or less 2-lipped). These present various transitions to the 5-toothed, fertile ray-flower found in the Cichorieae, on the one hand, and the 3-toothed, pistillate ray-flower found in the radiate tribes, on the other. *Myrypnois dioica* has the flowers all alike, with well developed corolla tube and short, rather deeply and irregularly 5-lobed ligule, which tends to be divided into a 2-lobed and a 3-lobed segment. *Catamixis* has a typical cichoriaceous 5-toothed ligule, but is otherwise similar to the Mutisieae rather than to the Cichorieae. *Mutisia* and a number of other genera have the marginal flowers pistillate, with a well developed, 3-lobed ligule, and usually with 2 much shorter, narrow lobes apparently opposite the ligule at the orifice of the tube. When these two shorter lobes are obsolete, as is not infrequently the case, the pistillate corollas are essentially similar to those regularly found in the radiate tribes.

Thus on the basis of corolla-form the Mutisieae commend themselves as a basic type, from which the ligulate, discoid, and radiate tribes could all have been developed. Unfortunately for this facile suggestion, the Mutisieae do not appear to be primitive in any other respect. The scarcely

leafy involucres, the mostly tailed anthers, the partly connate style-branches, the mostly naked receptacle, and the mostly numerous, often plumose pappus-bristles all appear to be advanced characters within the family. None of the radiate tribes shows any close approach to the Mutisieae, so that the species and genera of the Mutisieae which show stages transitional to the 3-lobed ligule are interesting as examples of how the process can occur rather than as ancestral forms. A relationship to the Cichorieae is clearly indicated by the ensemble of characters, however.

The Cichorieae are the most strongly marked tribe of the Compositae, and have sometimes been treated as a separate family. None of the features which distinguish the Cichorieae from the other tribes is without exception, however. The ligulate heads are matched in *Myrypnois*, of the Mutisieae. The latex canals are found in *Berardia* and *Warionia*, of the Cynareae, and *Gundelia* and *Gazania* of the Arctotideae (Col, 1904). Scattered species of genera in other tribes, although without the complex system of anastomosing canals, produce greater or lesser amounts of latex, sometimes (*Chrysothamnus, Parthenium*) enough to excite interest as a source of rubber.

Col (1899 et seq.) has noted that the resin ducts of the Compositae are different from the latex channels in position and anatomy. Although the elaboration of the latex system is usually associated with reduction of the resin system, it is possible to have both more or less developed in the same plant, or to have the resin system more or less reduced without the development of latex. If the ideas here expressed as to phylogeny and relationships of the tribes are correct, then the primitive Composite had a well developed system of resin-ducts and no latex. A curious bit of confirmatory evidence is provided by the fact that when the latex system is present in part but not all of the stem it is regularly better developed near the top, while the reverse is true of the resin system. This is exactly what should be expected under the evolutionary principle that the expression of a mutant gene and the resultant change in characteristics may appear at any stage in ontogeny, so that the older or first-produced parts are more likely to retain the primitive features.

The pollen grains of the Cichorieae commonly have the spines basally confluent into pronounced ridges, which enclose 6-21 spineless lacunae, so that the grain appears angular, rather than spherical as in most Compositae (Wodehouse, 1935, 1945). This condition is approached by *Vernonia* and a few genera in other tribes, but the ridges and lacunae are more numerous (30 or more) so that the grain retains its spherical appearance (Wodehouse, 1928a, 1928c, 1935). The similarity to the Vernonieae would seem to be a case of parallelism, rather than indicating the derivation of one tribe from the other. The occurrence of similar evolutionary developments does of course lend its bit to the assumption of a relationship between the tribes.

The most interesting genus of the Cichorieae, from a phyletic standpoint, is *Fitchia*, a group of a few woody species with imbricate involucre, chaffy receptacle, firm-awned pappus, and mostly opposite leaves, characters which recall the Heliantheae. Wodehouse (1935) points out that the pollen is similar to that of the Heliantheae, and not at all like that of most other Cichorieae. Similarly heliantheous pollen is found in some species of

the unmistakably cichoriaceous genus Soroseris (Stebbins, 1940), however, and the ligulate heads and 5-toothed rays of *Fitchia* are so characteristic of the Cichorieae that the genus must be included in that tribe. (The only other possibility would be the Mutisieae, which have been noted above to attain, rarely, the ligulate condition of the head, but the genus would be even more anomalous here.) The characters of *Fitchia* lend considerable support to the hypothesis that the Heliantheae represent the basic group of the Compositae. In view of the ensemble of features which suggest that *Fitchia* is the most primitive surviving genus of its tribe, a study of its wood-anatomy might throw some light on the question of whether there are any primitively woody members of the Compositae.

Thus, while the Cichorieae stand off more sharply from the rest of the Compositae than does any other tribe or group of tribes, they are clearly related to the rest of the family, and the morphological distinction is far from absolute. Their segregation as a separate family is therefore unnecessary, and in my opinion also unwise.[3]

The Vernonieae, as noted above, are allied to the Cynareae. They are also related to the Mutisieae. The genus *Stokesia*, which is generally referred to the Vernonieae, is anomalous in having the corollas of at least the outer flowers ligulate and rather deeply 5-lobed, while the innermost flowers, likewise deeply 5-lobed, are essentially regular. In the nature of the corollas it thus resembles the Mutisieae, and differs from all the other Vernonieae, but the anthers, styles, and pollen are those of the Vernonieae.

The Eupatorieae appear to be related to the Vernonieae, from which they differ chiefly in their obtuse or clavate, merely papillate styles, basally obtuse rather than sagittate anthers, frequently opposite or even whorled leaves, and non-lophate pollen. No transitional genera are known to me. The Eupatorieae are also approached by some of the Senecioneae, sufficiently so that one genus (*Adenostyles*) which has regularly been placed in the Eupatorieae probably belongs more properly to the Senecioneae. Robinson (1913) excluded *Adenostyles* from the Eupatorieae, and referred it to the Senecioneae, but his disposition of the genus, concurred in by Rydberg (1924) has otherwise apparently attracted little notice. *Adenostyles* conforms to all of the essential characters of the Eupatorieae, including the discoid, cyanic to white heads, and obtuse, merely papillate style-branches. It has no evident relative in the tribe, however, and its uniseriate, calyculate involucre is quite typical of the Senecioneae. *Adenostyles* is habitally very similar to the *Tussilago* group of the Senecioneae, and the

3 Dr. G. L. Stebbins' important contribution to our understanding of the Cichorieae (A new classification of the tribe Cichorieae, family Compositae. Madrono 12:65-81. 1953) appeared subsequent to the preparation of this paper. His remarks are in general agreement with the comments here made on the tribe, except that he would establish a separate, monogeneric tribe for *Fitchia*, to the list of whose primitive characters he adds the well developed vascular system of the corolla. Stebbins' belief that "the ancestors of the Cichorieae become separated from the ancestors of the rest of the Compositae at a very early date in the evolution of the family," would however seem wholly compatible with the treatment here presented, in which *Fitchia* is retained as a primitive member of the Cichorieae, apparently transitional to the ancestral Heliantheae.

Dr. Stebbins also points out that a number of American genera of the Cichorieae have echinate rather than echinolophate pollen, thus further reducing the morphological gap between the Cichorieae and the rest of the family.

principal technical difference between *Adenostyles* and *Homogyne* lies in the discoid heads of the former and merely disciform heads of the latter. Even the style is matched by that of *Homogyne*, which Bentham properly keeps with the *Tussilago* group in the Senecioneae, instead of with the Eupatorieae, because its disciform rather than discoid heads would make it anomalous in the latter tribe. Bentham also remarks on the evident relationship of *Homogyne* to *Tussilago*, which with its yellow corollas, evident rays, and sterile disk-flowers would be quite impossible in the Eupatorieae. *Tussilago* and its ally *Petasites* have the style-branches fused, as so frequently among groups with sterile disk-flowers, so that no information as to affinities is obtainable from their styles. Discoidy is no bar to admission to the Senecioneae or any of the other radiate tribes, and the *Tussilago* group itself contains a discoid genus (*Luina*). Since eupatorious styles, cyanic to white flowers, and discoid heads are already known to occur in the *Tussilago* group of the Senecioneae and (except for the styles) elsewhere in the Senecioneae as well, no extension of the limits of the tribe or subtribe is necessary in order to include *Adenostyles*. On the basis of the traditional taxonomic characters, therefore, *Adenostyles* could be included in either the Senecioneae or the Eupatorieae, but its apparent relatives are exclusively among the Senecioneae. Strong additional evidence for putting it in the Senecioneae is provided from another source. Col (1904) has shown that the resin-ducts in *Adenostyles* are external and adjacent to the vascular bundles, as in the Senecioneae (including among other genera *Petasites*, *Homogyne*, and *Tussilago*), rather than interposed between the bundles, as in the Eupatorieae.

The link between the Eupatorieae and Senecioneae provided by *Adenostyles* seems to be purely morphologic rather than phyletic, however. Not only is *Adenostyles* without apparent relatives in the Eupatorieae, but it would seem impossible to derive the imbricate involucres so commonly found in that tribe from the uniseriate, calyculate involucre of *Adenostyles*. Subuniseriate involucres occur in species of *Eupatorium* and elsewhere in the tribe, but these appear to have been derived independently from ancestors within the tribe with imbricate involucres. Since we have already noted a possible connection between the Vernonieae and some of the more primitive Senecioneae, and apparent relationship between the Eupatorieae and Vernonieae, it is not impossible that the Eupatorieae relate to the Heliantheae through the primitive Senecioneae. It would then not be surprising to see tendencies similar to those of the Eupatorieae appearing elsewhere in the Senecioneae.

It should be evident from the foregoing discussion that the radiate tribes are all closely allied, through the Heliantheae, that the discoid tribes are connected to the radiate tribes through the Arctotideae and possibly also through the Senecioneae and Heliantheae, that the discoid tribes are related to each other and to the Mutisieae, that the Mutisieae are also allied to the Cichorieae, and that there is an apparent link between the Cichorieae and the Heliantheae. Thus all of the tribes of the Compositae are inextricably related to each other, and on the basis of present information the Compositae must be considered a natural group.

A diagrammatic presentation of the ideas here developed as to the relationships of the tribes is attempted in fig. 1. Insofar as is possible on a

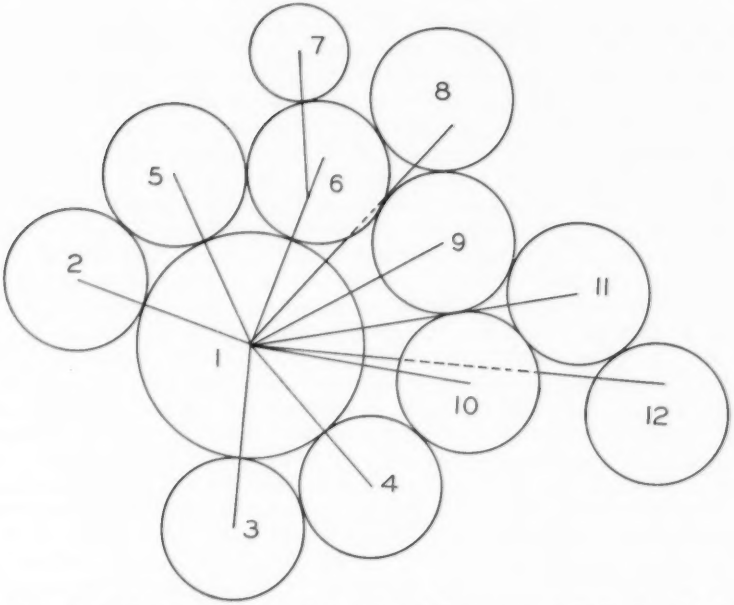

Fig. 1.—Probable relationships of the tribes of Compositae. 1. Heliantheae. 2. Astereae. 3. Anthemideae. 4. Arctotideae. 5. Inuleae. 6. Senecioneae. 7. Calenduleae. 8. Eupatorieae. 9. Vernonieae. 10. Cynareae. 11. Mutisieae. 12. Cichorieae.

2-dimensional representation, the tribes are juxtaposed to their apparent relatives. The probability that most of the tribes are related to each other through the Heliantheae or helianthoid ancestors is suggested by the series of lines radiating from the Heliantheae to other tribes. Were a three-dimensional representation possible, the Eupatorieae and Cichorieae would be so placed that the lines connecting them to the Heliantheae did not pass through any other tribe, and the Eupatorieae would be placed slightly closer to the Heliantheae than are the Vernonieae. It is doubtless an oversimplification to show all of the lines radiating directly from a single point, but the limitations of our knowledge as well as of the medium of presentation make any attempt at greater accuracy unwise at present.

Backed by some understanding of the morphology, relationships, and evolutionary trends within the family, one can proceed to consider the possible origin and relationships of the group as a whole. Traditionally the Compositae have been considered allied to the Campanulaceae, and in the Englerian system they are even put in the same order. The Composite-like heads of *Jasione*, the connate anthers and milky juice of the Lobelioideae, and the vegetative resemblance of various campanulaceous species to diverse species (especially among the Cichorieae) of the Compositae together might seem to indicate a relationship. Against such a relationship is the fact that the similarities are between advanced members of the two groups. The primitive, opposite-leaved Heliantheae scarcely seem derivable from anything in the Campanales. Starting with the as-

sumption that the Campanulaceae are the nearest relatives of the Compositae, and that the primitive characters in the Compositae should be so chosen as to represent an approach to the Campanulaceae, Leonhardt (1949) arrived at the most unlikely conclusion that the Cynareae are the most primitive tribe in the family. In view of the much closer resemblance especially of the more primitive Compositae to some other families, and the embryological differences between the Compositae and Campanulaceae cited below, I do not believe that the assumption of a relationship to the Campanulaceae can be upheld.

Two small families with capitulate, involucrate inflorescences and one-seeded fruits have frequently been mentioned as possible allies of the Compositae. These are the Calyceraceae and Dipsacaceae. Any possibility of their being ancestral to the Compositae is removed by the fact that both have the single ovule pendulous from the top of the ovary, while in the Compositae the ovule is basally attached. Of the two, the Calyceraceae are perhaps the more similar to the Compositae, but since the relationships of the Calyceraceae are also in doubt they throw little light on the problem.

The Dipsacaceae are further removed from any possibility of being ancestral to the Compositae by the fact that they consistently have only 4 or fewer stamens. The Dipsacaceae have customarily been assigned to the Rubiales, near the Valerianaceae, and I know of no reason to challenge this disposition. Any possible relationship of the Dipsacaceae to the Compositae would imply the origin of both families from more generalized rubialian ancestors. Although the lack of transitional forms makes such an assumption dangerous, it certainly does not seem impossible. The 4-stamened condition of the Dipsacaceae is obviously a reduction from a 5-stamened condition, and both types of ovular attachement, with all intermediates, are known in the Rubiaceae. The connate condition of the anthers in the Compositae is obviously derived from the more common angiospermous condition in which they are free. The imbricate aestivation of the corolla-lobes in the Dipsacaceae is likewise no barrier to a common ancestry between the families, since imbricate, contorted, and valvate aestivations are all known in the Rubiaceae. Similar evolutionary forces working on a generalized rubialian ancestor might very well produce in one case the Dispsacaceae, and in another the Compositae. The pappus-like calyx of *Valeriana,* the differentiation of the marginal flowers of the inflorescence in *Viburnum,* the tendency in the Rubiaceae toward a 2-carpellate ovary and in the Valerianaceae toward a uniovulate ovary are all features which suggest that the evolutionary tendencies which led to the development of the Compositae exist in other Rubiales in addition to the Dipsacaceae.

The Compositae have been noted by a number of students to be unlike the Campanulaceae and their allies in embryological features (using this term in its broadest sense, including the steps leading to pollen-formation), but very similar to the Rubiaceae and Dipsacaceae (Schurhoff, 1926; Schnarff, 1933; Poddubnaja-Arnoldi, 1933). The limited number of species that have been studied necessitates some caution in drawing conclusions from these investigations, but the data are certainly not without significance.

As against a relationship to the Rubiaceae, Hutchinson (1948) points

out that in the latter family the guard-cells and stomata are surrounded by specialized epidermal cells, while in the Compositae they are surrounded by ordinary epidermal cells. Should these features prove constant in the two families it would suggest again that any relationship is through a common ancestor rather than directly. The Dipsacaceae and Valerianaceae, however, commonly have a stomatal apparatus similar to that of the Compositae, and types similar to both the Rubiaceae and the Compositae can be found in the Caprifoliaceae (Metcalfe & Chalk, 1950), so that if the order Rubiales is accepted in its customary definition the stomata raise no barrier to relationship with the Compositae.

In my opinion the Compositae are probably more closely related to the Rubiales than to any other order, but the evidence is as yet far from conclusive.

Bessey's charts (1897, 1916) of the relationships of the orders of angiosperms disposed of the problem of the resemblance of the Compositae to both the Rubiales and the Campanales by deriving both the Campanales and the Compositae (Asterales) from the Rubiales. Most modern authors, however, have not considered the Campanales and Rubiales to be closely allied. In this vein, Dr. Rogers McVaugh, whose competence as a student of the Campanales is well known, writes to me that in his opinion "the Rubiaceae and Campanulaceae . . . have come from different stocks. If both have contributed to the Compositae then I suppose it follows that the later are of quite mixed origin." Barring some radical change in our understanding of the evolutionary relationships in the Sympetalae, the facile solution that the dual resemblance of the Compositae is due to a close relationship between the two groups which it resembles cannot be adopted. It is even more difficult to consider the Compositae to be an artificial rather than a natural group. One can scarcely believe that convergent evolution from diverse sources could have produced such a thoroughgoing structural similarity. I know of no serious student of the family who has questioned its naturalness, and I am convinced that no such question can be sustained.

Stebbins (1950) has recently suggested that:

> "students of angio-sperm phylogeny should look for traces of an ancient polyploidy resulting from hybridization between species which were the ancestral prototypes of many of our modern families. The reticulate pattern of evolution which is the typical one when allopolyploidy has occurred should characterize the inter-relationships between families and orders of flowering plants. If this is actually the case, the explanation might be at hand for the fact that botanists have had much . . . difficulty in deciding on the true inter-relationships between the families and orders of flowering plants. . . ."

Such a hypothesis carries as a necessary corollary the rapid divergence of the original angiosperms into lines which represent the basic family groups of the present, so that morphologic differences which now generally separate families were once associated with species and genera instead. This corollary, which by itself has long been attractive to me, is further elaborated by Stebbins in the same work. What little evidence is available from the cytology of the Compositae may be compatible with these suggestions. *Wyethia* (Weber, 1946) and *Rudbeckia* (Battaglia, 1946), which are among the more primitive living genera of the family, have a basic chromosome-number of n=19. The numbers found in related, probably more advanced members of the tribe, such as 18 in *Enceliopsis*, 17 in

Helianthus and 15 in *Helianthella* (Weber, 1952), seem to indicate a consistent reduction in chromosome-number, correlated with morphological divergence and specialization. The number 19 is so high as to indicate a probability of polyploidy, and the fact that the highest known number in the series is an odd number suggests that alloploidy rather than autoploidy may have been involved. However, the lower counts of n=8 (Weber unpubl.) and n=11 (Battaglia, 1946), respectively, in the also closely allied genera *Viguiera* and *Echinacea,* suggest that the polyploidy may have followed rather than accompanied the origin of the family. Thus the application to the Compositae of Stebbins' hypothesis of rapid differentiation of the angiosperm families, accompanied by polyploidy, would be premature at present. More evidence both within the Compositae and also as to its general applicability in other groups will be necessary before the inviting prospects of Stebbins' hypothesis can be realized.

The above evidence from chromosome-numbers in the Heliantheae may also be compatible with the bizarre and generally rejected hypothesis of Anderson (1934) that the angiosperms originated by amphiploidy between something related to the Cycadales (n=12) and something related to the Gnetales (n=7), followed by a rapid differentiation of the principal families. This hypothesis, since it likewise calls for the differentiation at the specific and generic level of what are now the principal families of angiosperms, avoids much of the difficulty raised by the resemblance of the Compositae to two presently very different groups. Even more than with Stebbins' hypothesis, however, Anderson's hypothesis cannot be fully accepted here until support for its basic premise is forthcoming.

SUMMARY

The ancestral prototype of the Compositae is considered to have been an opposite-leaved herb, with few, many-flowered heads, leafy, several-seriate involucre, chaffy receptacle, pistillate, fertile, yellow rays, perfect, yellow disk-flowers with the midvein of the lobes developed, a chaffy pappus of 5 members, connate, tailless anthers, and without well differentiated stigmatic lines on the style-branches. No presently existing genus combines all these features, but if such a plant existed it would be placed in the Heliantheae. The genus *Wyethia,* although it has alternate leaves, perhaps comes as near as any existing genus to the hypothetical prototype.

The traditional 13 tribes of the Compositae, save only the Helenieae, represent natural groups, defined by the usual association of several independently variable features. The Helenieae, which have been distinguished from the Heliantheae solely by th absence of chaff from the receptacle, are an artificial assemblage of several subtribes of the Heliantheae which have separately lost the receptacular chaff. Each of the other radiate tribes appears to be derived separately from the Heliantheae, except for the Calenduleae, which are an offshoot of the Senecioneae. The three discoid tribes, plus the Mutisieae, stand apart as a group from the radiate tribes, although there is an obvious relationship between the Arctotideae and the Cynareae and a more doubtful one between the Senecioneae and Vernonieae. The Cichorieae are allied to the Mutisieae and apparently also to the Heliantheae. None of the discoid, bilabiate, or ligulate tribes can be considered ancestral to any of the others. They are related instead through

a common ancestor which, even though probably discoid, could only with difficulty if at all be excluded from the Heliantheae.

The evolutionary tendencies operating in the inflorescence of the Compositae can mostly be grouped under the headings of aggregation and reduction. These represent merely a continuation of the trends which led to the development of the Compositae from their more generalized sympetalous ancestors. Natural selection appears to be insufficient as the sole explanation for these tendencies, which sometimes proceed beyond the limit of survival-value.

The Compositae are a wholly natural group, probably eventually related to the Rubiales, although the evidence of relationship is not conclusive. Attempts to explain the resemblance of the Compositae to both the Rubiales and the Campanales, either by assuming a close relationship between the latter two groups, or by invoking an ancient polyploidy followed by a rapid differentiation of lines leading to the present day families of angiosperms, are not considered acceptable at this time. The lack of any real connecting links, and the necessity to consider the resemblance to the Campanulaceae as purely fortuitous, suggest the need for some reserve in accepting the derivation of the Compositae from the Rubiales.

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Book Review

AMPHIBIANS AND REPTILES OF WESTERN NORTH AMERICA. By Robert C. Stebbins. McGraw-Hill Book Co., New York. 1954. 528 pp., 104 pls. $8.50.

If a naturalist, an artist, a college professor, and a perfectionist were to collaborate in the compilation of a book, we would expect a volume of outstanding merit. That is exactly what we have here, but our author is not four, but only a single person, albeit a skilled one who has made full use of his many talents. He is Associate Professor of Zoology at the University of California (Berkeley), a field naturalist of note, a competent artist, and a man who pays attention even to the most meticulous detail. Add to these his Curatorship of Herpetology at the Museum of Vertebrate Zoology, and the sum total is a background without peer for a book that doubtless will long remain the standard for its subject and geographic range.

The area embraced by this ambitious work includes the states and provinces of New Mexico, Colorado, Wyoming, Montana, Saskatchewan, Mackenzie, and all the other political divisions westward to the Pacific Coast, even Alaska. Within the borders of this vast domain live one hundred ninety-four species of salamanders, frogs, toads, turtles, lizards, and snakes, plus a multitude of subspecies. For each species there is a description, suggestions on where to look for specimens, notes on habits (including breeding), a distribution map, and selected references. Every species is illustrated by excellent line drawings. The dichotomous keys for identification are accompanied by numerous sketches pointing up details of anatomy or pattern that are of diagnostic value. Used in conjunction with the keys, the sketches serve their purpose admirably, but, since none of the drawings is labelled, quick identification by comparing animal with picture is not possible.

There is one major defect—the sort of unfortunate omission that probably is more chargeable to an editor than to an author. There is no direct cross-index between the text and the maps, and the maps, which are assembled in groups, the better for quick comparison, are, in general, far removed from the text accounts. A page reference under each map, indicating the text account of the same species (and vice versa), would have greatly increased the usefulness of the book.

The introduction includes such a competent review of methods of collecting and of techniques for preserving and storing specimens that even the experienced field or museum man may read it with profit.

Our author, experienced in teaching and adroit at separating grain from chaff, has packed an incredible amount of information into his book. It is a *must* item for all naturalists interested in western North America, and it should be acquired at once by all libraries of the region whose clients are of high school or college level.—ROGER CONANT, Philadelphia Zoological Garden, Philadelphia.

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